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Reproductive performance and fetal development of white-tailed deer *(Odocoileus virginianus)* in southwestern Manitoba.

By Soprovich, Daniel W. 1991.

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ABSTRACT

White-tailed deer were collected in southwestern Manitoba from 1976-77 to 1984-85 to examine reproductive performance. Fawns had a fetal rate of 1.12 fetuses/pregnant doe, 30.5% of the fawns were pregnant, and twins were recorded from 3 does. The pregnancy rate of adult does was 98.0% and appeared to be greater than that of yearlings. The fetal rate of adult does (2.03) was greater than that of yearlings (1.67). Annual variation in fetal rate was not found for adults but was suggested for yearlings. As annual variation in gross productivity is non-existent or minor, such data serve little purpose for population management. Fetal sex ratio did not differ from 50:50 for the complete data set. Visual femur fat of pregnant and non-pregnant fawns was related to cumulative snow depth. Body weight was inversely related to cumulative snow depth for pregnant fawns but not for non-pregnant fawns, and was greater for pregnant fawns at zero cumulative snow depth. Body weight correlated with time for non-pregnant fawns. It was hypothesized that this apparent differential impact of winter severity on pregnant and non-pregnant fawns would tend to stabilize density. Fetal linear growth in doe fawns may be slower than growth rates reported in the literature. Substantial size variation sometimes occurs among siblings from adult does. Fetal linear growth in adult does was not influenced by sex or litter size; however, the method used to estimate growth rate and the sampling regime may have been responsible for this result. Fetal linear growth in adults appears to be faster than reported in does from Michigan; however, further data are required to verify this. In adult does, linear fetal growth to forehead-rump length <380 mm was impacted negatively by cumulative snow depth. Conception date can be estimated incorrectly with use of an incorrect growth function or due to fetal growth which is impaired by doe condition. Fetal linear growth did not differ between yearling and adult does; however, the sample from yearlings was small and the estimate of fetal growth rate imprecise. The relationship between fetal weight and length best fit a power model for both yearling and adult does. No sex or age effect could be detected for this relationship; however, the sample from yearling does was small.

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INTRODUCTION

Ransom (1964, 1966, 1967) examined the reproductive performance and seasonality of breeding in white-tailed deer (Odocoileus virginianus) from the Whiteshell, Turtle Mountain, and Duck Mountain areas of Manitoba. On the basis of fetal size data, Ransom (1966) suggested that does from the Whiteshell became pregnant earlier than those from the other areas, and speculated that this might be due to genetic or range quality differences. Additionally, Ransom (1964, 1967) suggested geographic, age-specific, and annual variation in the ovulation and fetal (fetuses/pregnant doe) rates of white-tailed deer. Unfortunately, the potentially confounding influences of geographic area, age of the doe, and year were not completely controlled by Ransom (1964).

In Manitoba, conception date has been estimated by determining fetal age from a growth function developed elsewhere (eg., Cheatum and Morton 1946 by Ransom 1966) and then backdating from the date of death. Consequently, it is necessary that the growth function be representative of fetal growth in white-tailed deer from Manitoba for estimates to be accurate. As investigation of white-tailed deer fetal growth rate is limited spatially, data are relatively few (Cheatum and Morton 1946, Verme 1963, Short 1970, Hamilton et al. 1985), and relationships may have been compromised by variation in the condition of does and other factors (Soprovich In press), the potential for significant inaccuracy exists. In recognition of this problem, Soprovich (In press) found that it was possible to accurately estimate growth rate from fetuses of unknown age, although the technique was sensitive to conception distribution and the type and distribution of a sample.

White-tailed deer productivity and other data were collected in southwestern Manitoba from 1976-77 to 1984-85. The objective of this program was to determine the impact of winter weather on productivity (Milliken 1978a) in an effort to develop a predictive capability for management of the white-tailed deer resource. The present study examined the productivity, environmental, and other data which resulted from this program. Additionally, application of the technique to estimate fetal growth rate (Soprovich In press) and other fetal growth data are presented.

METHODS

White-tailed deer which had died from diverse causes were obtained between 1976-77 and 1984-85 from an administrative region in southwestern Manitoba known as the Brandon Subregion (Milliken 1977a). The number of fetuses, fetus size (crown-rump length in mm, forehead-rump length in mm, weight in g), condition of the doe (visual femur fat as detailed by Cheatum 1949, general body condition), and age by tooth wear according to Taber (1963) for early years, Larson and Taber (1980) for later years, were determined for female deer. Fetal age and conception date were estimated with the growth function of Armstrong (1950) for fetuses from 1982-83 (Chranowski 1983a), Cheatum and Morton (1946) for fetuses from 1983-84 (Chranowski 1984a), and Ozoga and Verme (1985) for fetuses from 1984-85 (Chranowski 1985a). To minimize annual variation in estimation error, conception date in this study was estimated with 1 growth function (Short 1970) based on data from Verme (1963). Unless otherwise stated, each sibling was treated as an independent observation. Body weight was collected where possible for female fawns (Milliken 1977a). The deer examined in this study were collected between November and June with the majority of the sample from January to April (Milliken 1977a, Milliken 1978a, Milliken 1979a, Milliken 1980a, Milliken 1981a, Chranowski 1982a, Chranowski 1983a, Chranowski 1984a, Chranowski 1985a). As female fawns may become pregnant relatively late (Ransom 1964, Hall and Hall 1980, Kerr and Peterson 1988), only fawns collected between 1 January and 31 May were used to estimate pregnancy rate. Some data were not used due to uncertainty about the number of fetuses (eg., DB-19 from 1978-79) or age of the doe (eg., DB-23 from 1980-81 was aged as an adult by an individual not directly involved in the program; as yearlings are often classified as adults, this doe may have been a yearling). Additionally, fetal length data from 1981-82 and 1982-83 were excluded from growth analysis because they were collected incorrectly (D. J. Chranowski, Man. Dept. Nat. Resour., pers. commun.). Time was measured as the number of days between the beginning of November and the collection date (i.e., date = 1 for 1 November, date = 2 for 2 November, etc.).

For the same time period, data on winter weather severity were collected at a number of sites in southwestern Manitoba (Milliken 1977b, Milliken 1978b, Milliken 1979b, Milliken 1981b, Chranowski 1982b, Chranowski

1983b, Chranowski 1984b, Chranowski 1985b). At each site, snow depth was measured each week from the onset to disappearance of snow on the ground (for a more detailed explanation of the methodology for measuring snow depth see Milliken 1978b or Soprovich 1990). At other locations throughout the Brandon Subregion, the Atmospheric Environment Service, Environment Canada collected daily temperature data (Monthly Record Series) during the study period.

For those deer where the location and date of collection were known, data from the nearest weather severity monitoring station were used to construct a variable to model the impact of snow depth on white-tailed deer. The daily snow depth was estimated by interpolating between weekly measurements, which also facilitated use of the data when observations were missing (in which case interpolation occurred between adjacent datum in the time series). Addition of each estimated daily snow depth until the date of death (assumed to be the date of collection unless specified otherwise) yielded a variable called cumulative snow depth and measured in cm·day. This variable is a variant of the snow depth component used by Verme (1968) in his model of winter weather severity for white-tailed deer.

In several instances where a doe had been injured for some indeterminate period of time prior to her death, observations were not used for fetal growth rate analysis. For the analysis of fetal growth rate in adult does, one obviously incorrect observation was deleted for analysis (see Table 5), as were observations of twins or triplets where one or more siblings growth appeared to have been impacted by doe condition (i.e., the twins with forehead-rump lengths of 393 mm, 295 mm and 318 mm, 375 mm and the triplets from Table 5). Fetal growth rate was estimated from complete data sets and, because conception in southwestern Manitoba occurs over a time period ≈ 8 weeks in duration (Ransom 1964), modified data sets which attempted to minimize the impact of sampling bias on growth rate estimation (see **Estimation of Fetal Growth Rate**). The date by which the latest conceived fetus in the sample would have reached 63 mm (i.e., ≈ initiation of linear growth after data in Verme 1963) was estimated by addition of 58 days (i.e., after Short 1970) to the estimated date of conception of this fetus. Similarly, the date by which the earliest conceived fetus in the sample would have reached 380 mm (i.e, ≈ cessation of linear growth) was estimated by addition of 150 days to the fetuses' estimated date of conception. The modified data set consisted of fetuses collected from between these dates. This range should almost ensure

the availability for sampling of a complete distribution about any date and thereby minimize or eliminate sampling effects (Soprovich In press). Additionally, this procedure should produce a data set which is not unduly influenced by annual variation in the conception date distribution. For the analysis of fetal weight and length, data were fit to exponential, linear, logarithmic, and power models and singletons, twins, and triplets were not examined separately.

The data were analyzed using S.A.S. software on an Apple II+ computer or with software developed by the author on a Mind computer. Custom programing followed Mendenhall (1971) for the t test and Strickberger (1968) for the X^2 test. The Yates correction for continuity was used for the X^2 tests and simple regression analyses were for the linear model unless specified otherwise.

RESULTS

REPRODUCTIVE PERFORMANCE

Fawn Does

Twenty-five of the 82 fawns (30.5%) were pregnant, 3 of these fawns had twins, and the fetal rate was 1.12 fetuses/pregnant doe. The pregnancy rate for fawns killed during January (28.6%, n = 21) was not different (X^2 = 0.01, df = 1, P > 0.10) from that of fawns killed during February (25.0%, n = 20).

Yearling and Adult Does

The pregnancy rate of adult does (Table 1) was greater than that of yearlings (X^2 = 5.25, df = 1, P < 0.025). The pregnancy rate was not different (X^2 = 0.92, df = 1, P > 0.10) when observations of does with enlarged uteri but no fetuses were deleted from the yearling data set. The pregnancy rate of yearling does was not different (X^2 = 0.49, df = 1, P > 0.10) from that found by Ransom (1964). The adult fetal rate (2.03) was greater (one-tailed test, t = 3.70, df = 137, P < 0.005) than that of yearling does (1.67). Similarly, the mean number of fetuses per doe (pregnant and non-pregnant) was 1.99 for adults and 1.46 for yearlings.

The fetal rate of adult does was not different (z = 1.07, n_1 = 38,

Table 1. Pregnancy rate and number of deer with 1, 2, 3, or 4 fetuses for yearling and adult does from southwestern Manitoba for the years 1976-77 to 1984-85.

Age	Pregnancy rate, % (n)	Number of does[a]			
		1 fetus	2 fetuses	3 fetuses	4 fetuses
Yearling	87.5 (48)[b]	14	24	1	
Adult	98.0 (102)	11	74	12	1

[a]Number of does is not equal to number of pregnant does because fetuses could not be found for some pregnant does.
[b]Three does had an enlarged uterus but no fetus could be detected; they were treated as not pregnant.

n_2 = 98, P > 0.28) from that found by Ransom (1964) for the Turtle Mountain area ($\bar{x}$ = 1.92, n = 38, SE = 0.09). Annual fetal rates did not differ from Ransom's (1964) mean for adult does (Table 2). Additionally, annual variation in fetal rate was not apparent for adult does (ANOVA, F = 0.77, df = 8,91, P > 0.25).

Table 2. Mean fetal rate (fetuses/pregnant doe) of adult does from southwestern Manitoba for the years 1976-77 to 1984-85 with comparison to Ransom's (1964) estimate for adult does.

Year	n	Fetal rate	t[a]	df	P
1976-77	2	2.50	1.43	38	<0.20
1977-78	7	2.00	0.38	43	>0.20
1978-79	21	2.00	0.53	57	>0.20
1979-80	6	2.17	0.96	42	>0.20
1980-81	11	1.91	-0.06	47	>0.20
1981-82	6	2.17	1.04	42	>0.20
1982-83	25	2.12	1.36	61	<0.20
1983-84	6	1.67	-1.05	42	>0.20
1984-85	15	2.07	0.91	51	>0.20

[a]Statistical test was two-tailed; H_o: $\mu_1 = \mu_2$, H_A: $\mu_1 \neq \mu_2$.

For yearling does, the fetal rate was not different (t = 0.22, df =

43, $P > 0.70$) from that found by Ransom (1964) for the Turtle Mountain area ($\bar{x} = 1.71$, $n = 7$, $SE = 0.25$). Although annual fetal rates were not different from Ransom's (1964) mean (Table 3), yearling fetal rate varied between years (ANOVA, $F = 5.41$, $df = 6,31$, $P < 0.001$). The datum from 1976-77 was not used in the ANOVA because of a requirement for >1 observation per cell. Comparison of each year to the others resulted in 1 significant difference (1980-81 versus 1982-83, two-tailed test, $t = 2.27$, $df = 9$, $P = 0.05$).

Table 3. Mean fetal rate (fetuses/pregnant doe) of yearling does from southwestern Manitoba for the years 1976-77 to 1984-85 with comparison to Ransom's (1964) estimate for yearling does.

Year	n	Fetal rate	t[a]	df	P
1976-77	1	2.00	Undefined[b]	N/A	N/A
1977-78	3	1.00	-1.80	8	<0.20
1978-79	5	1.80	0.26	10	>0.20
1979-80	3	1.00	-1.80	8	<0.20
1980-81	4	1.50	-0.53	9	>0.20
1981-82	0				
1982-83	7	2.14	1.50	12	<0.20
1983-84	6	2.00	1.07	11	>0.20
1984-85	10	1.50	-0.73	15	>0.20

[a]Statistical test was two-tailed; H_0: $\mu_1 = \mu_2$, H_A: $\mu_1 \neq \mu_2$.
[b]Variance not defined for a sample of 1.

Fetal sex ratio (Table 4) did not differ from 50:50 for yearling ($X^2 = 0.06$, $df = 1$, $P > 0.80$) or adult ($X^2 = 0.01$, $df = 1$, $P > 0.80$) does.

Table 4. Number of male and female fetuses from yearling and adult does from southwestern Manitoba for the years 1976-77 to 1984-85.

Age	Number of males	Number of females
Yearling	9	7
Adult	47	48

CONDITION, BODY WEIGHT, AND PREGNANCY IN FAWNS

Visual Femur Fat and Pregnancy

Visual femur fat (%) was related to cumulative snow depth (Fig. 1, 2) for pregnant ($r^2 = 0.61$, $F = 33.87$, $df = 1,22$, $P < 0.001$) and non-pregnant fawns ($r^2 = 0.43$, $F = 36.50$, $df = 1,48$, $P < 0.001$). Cumulative snow depth was utilized in the analysis because it had previously been established that a linear trend existed between these variables; however, cumulative daily temperature is strongly correlated with cumulative snow depth (D. W. Soprovich, unpubl. data) and could have been used as an independent variable. A relatively large proportion of non-pregnant fawns were in poor condition (eg., 15/50 non-pregnant fawns versus 1/24 pregnant fawns had visual femur fat ≤10%). Visual femur fat of pregnant fawns was reasonably high to ≈ 3500 cm·day. In contrast, several non-pregnant fawns had very low (≤10%) visual femur fat levels at low cumulative snow depth.

The regression line for pregnant fawns ($B_1 = -0.0092$) was less steep than that for non-pregnant fawns ($B_1 = -0.0131$); however, the 2 slopes were not different (assumption of heterogenous variance, $F = 2.11$, $df = 1,59$, $P \approx 0.15$). The intercepts of the lines were almost identical for pregnant (81.5%) and non-pregnant fawns (81.1%).

Body Weight and Pregnancy

Weight and cumulative snow depth (Fig. 3, 4) were related for pregnant fawns ($r^2 = 0.42$, $F = 11.52$, $df = 1,16$, $P < 0.005$) but not for non-pregnant fawns ($r^2 = 0.08$, $F = 3.30$, $df = 1,36$, $0.05 < P < 0.10$). For any range of cumulative snow depth, body weight was highly variable among the non-pregnant fawns. The intercept of the regression line was greater (one-tailed test, $t = 2.23$, $df = 52$, $P < 0.025$) for pregnant fawns (41.5 kg) than non-pregnant fawns (36.1 kg). Body weight declined fast for pregnant fawns ($B_1 = -0.00199$) relative to non-pregnant fawns ($B_1 = -0.00106$); however, the slopes were not different (assumption of homogenous variance, $F = 1.26$, $df = 1,48$, $P = 0.27$). The regression lines intercepted at 29.9 kg and 5806 cm·day, a cumulative snow depth greater than recorded for pregnant fawns.

Although the multiple coefficient of determination increased from 0.42 to 0.46, body weight of pregnant fawns was not related to the number of days since 1 November ($t = -1.08$, $df = 15$, $P \approx 0.30$) for a multiple linear regression (backwards elimination) analysis with cumulative snow depth and

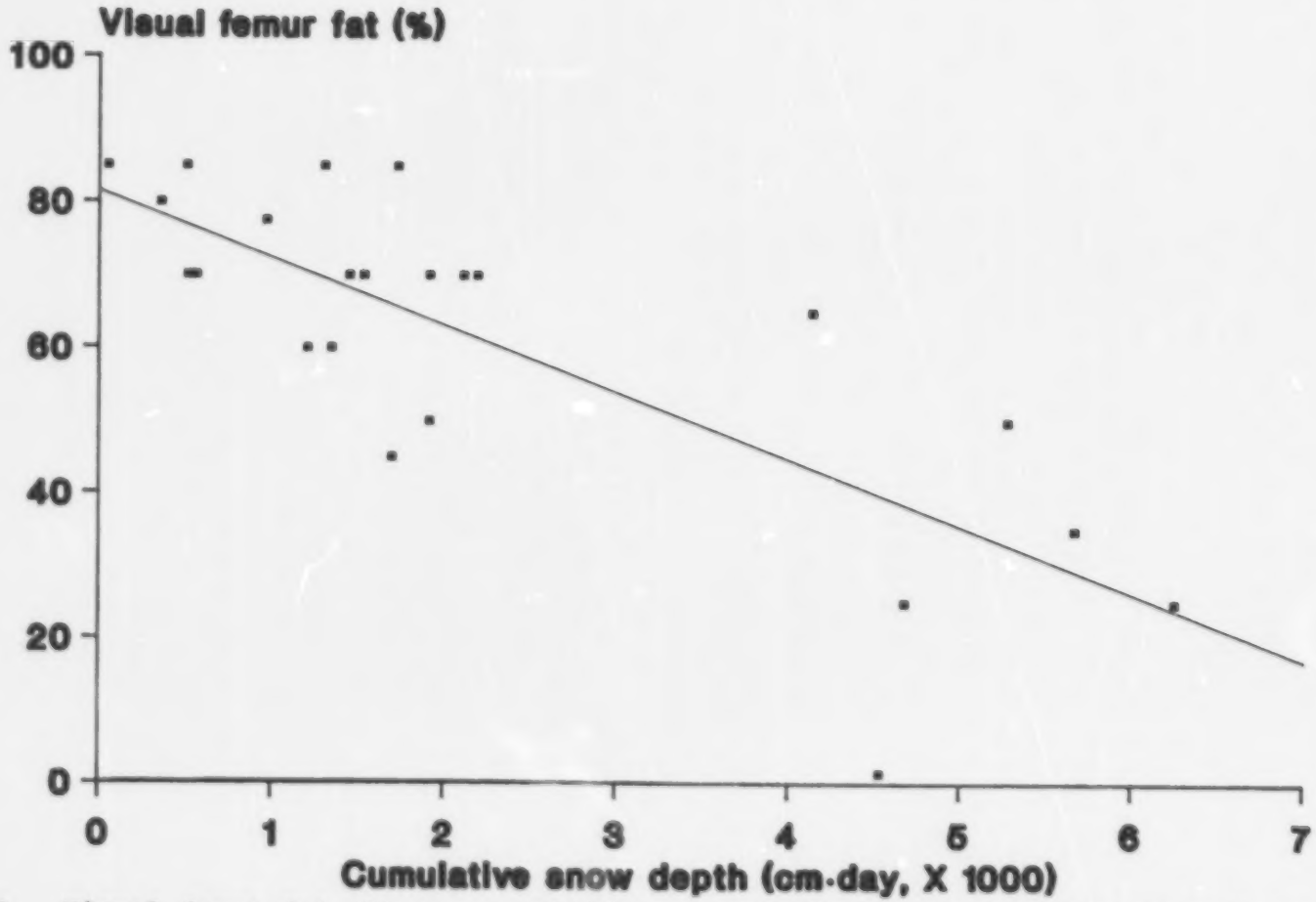

Fig. 1. Visual femur fat (%) vs. cumulative snow depth (cm·day, X 1000) of pregnant fawn white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Regression line significant at $P < 0.001$.

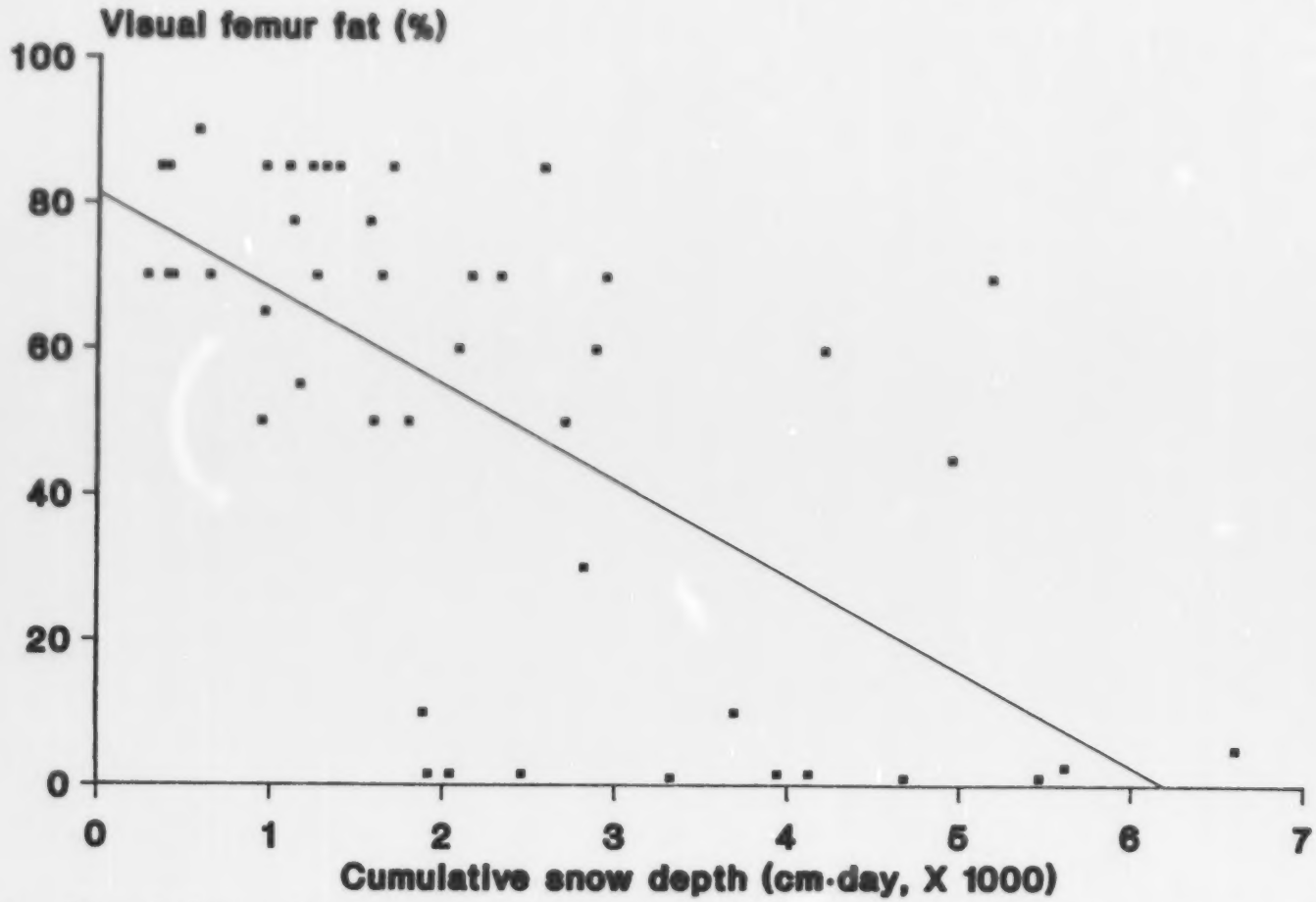

Fig. 2. Visual femur fat (%) vs. cumulative snow depth (cm·day, X 1000) of non-pregnant fawn white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Regression line significant at $P < 0.001$.

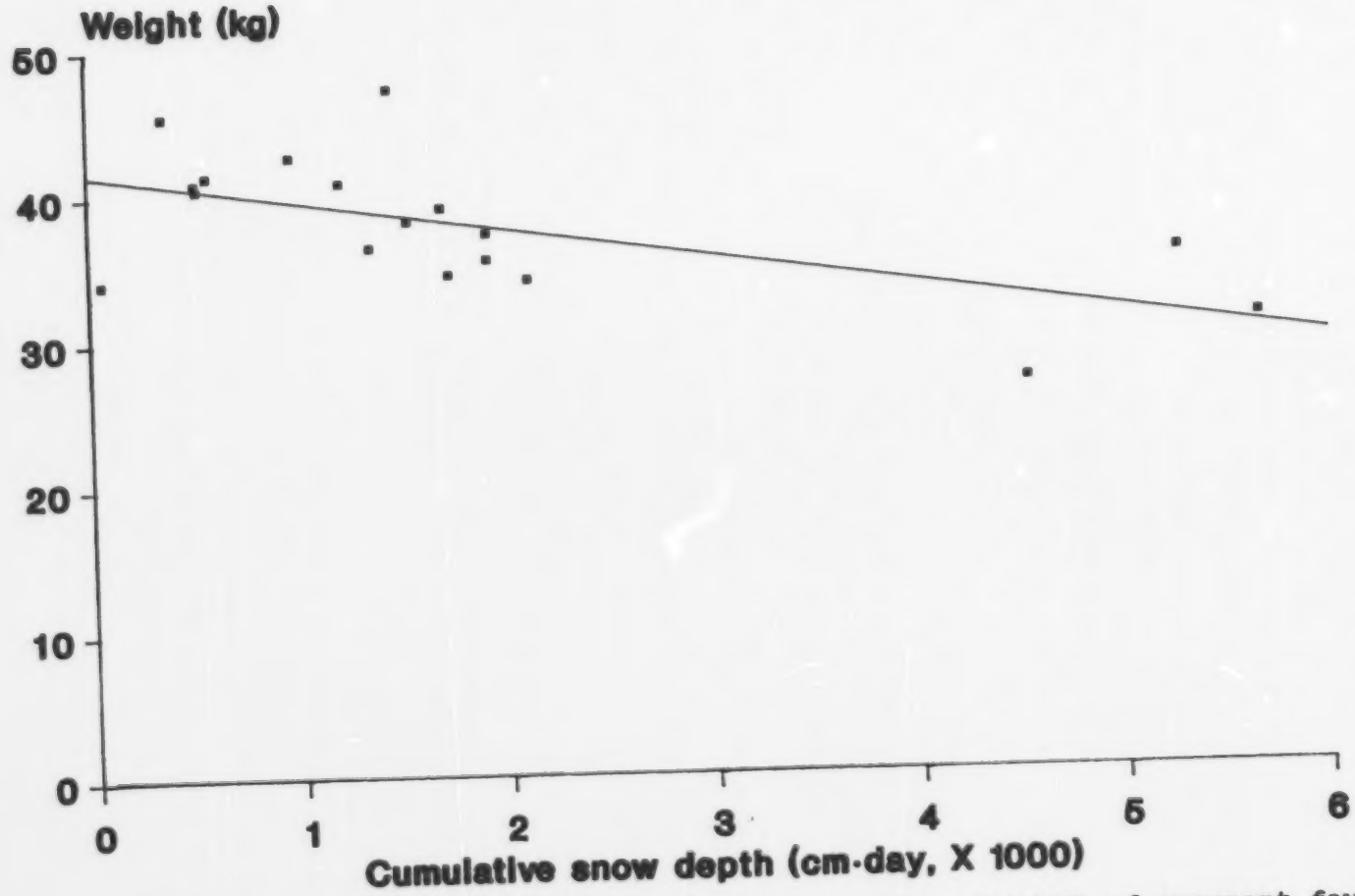

Fig. 3. Body weight (kg) vs. cumulative snow depth (cm·day, X 1000) of pregnant fawn white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Regression line significant at $P < 0.005$.

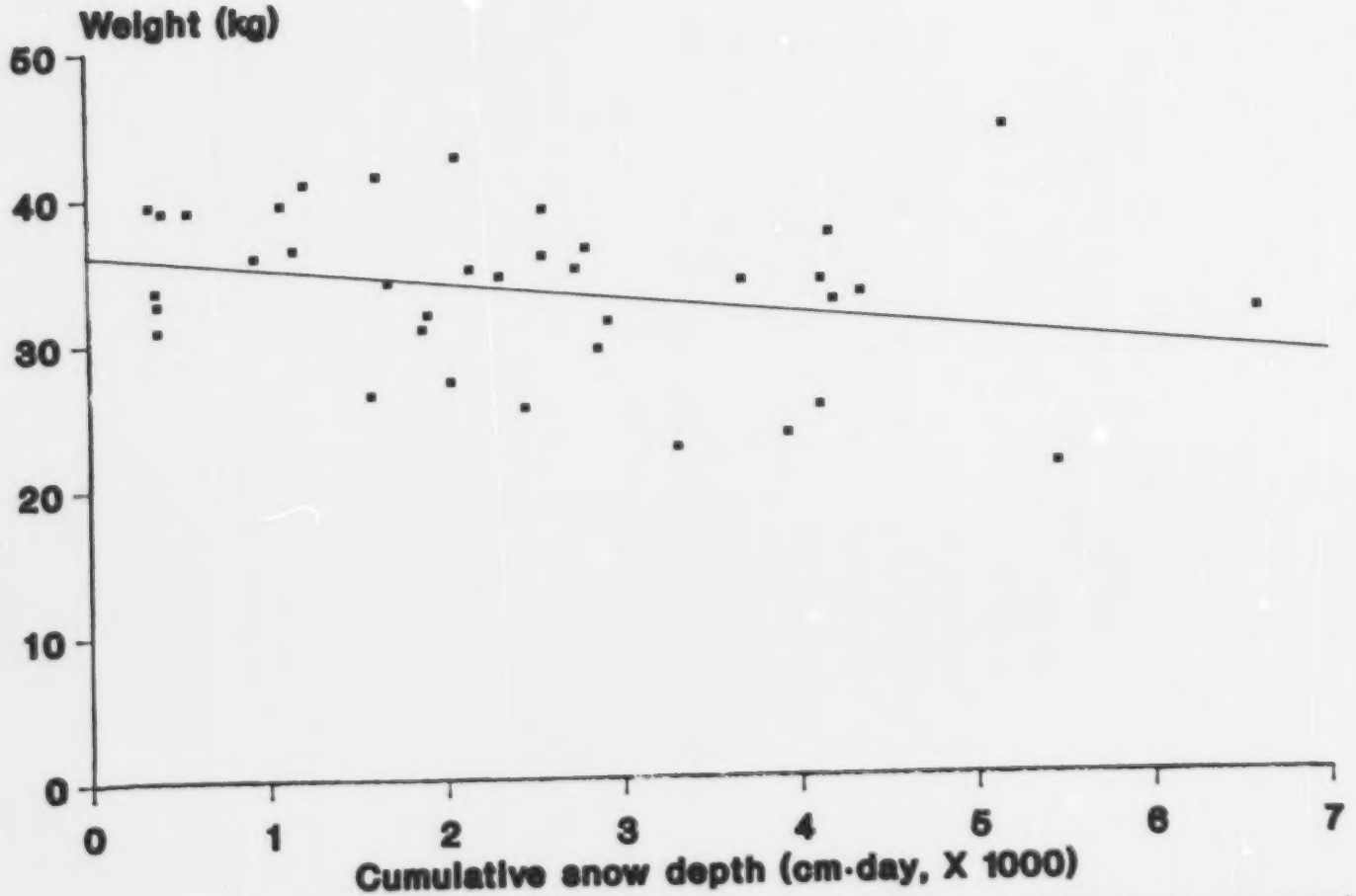

Fig. 4. Body weight (kg) vs. cumulative snow depth (cm·day, X 1000) of non-pregnant fawn white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Regression line not significant at $P < 0.05$.

number of days since 1 November as independent variables. Body weight and number of days since 1 November were correlated for a simple regression model (r^2 = 0.39, F = 10.08, df = 1,16, P < 0.01) which was not improved by the addition of cumulative snow depth (t = -1.44, df = 15, P < 0.20 for two-tailed test and P < 0.10 for one-tailed test). For non-pregnant fawns, weight and the number of days since 1 November were related (r^2 = 0.26, F = 12.78, df = 1,36, P ≈ 0.001) in the multiple regression analysis and addition of cumulative snow depth (P > 0.25) increased the multiple coefficient of correlation minimally. With the number of days since 1 November as the independent variable, the slopes of the regression lines were not different (assumption of homogenous variance, F = 0.01, df = 1,50, P > 0.25) for pregnant (B_1 = -0.112) and non-pregnant (B_1 = -0.116) fawns. Similarly, the intercepts were not different (t = 0.66, df = 52, P > 0.25) for pregnant (B_0 = 50.7 kg) and non-pregnant (B_0 = 46.8 kg) fawns.

Observations of pregnant fawns from high cumulative snow depth were few relative to non-pregnant fawns (eg., 16.7%, n = 18 versus 50.0%, n = 30 from cumulative snow depth >2200 cm·day). For cumulative snow depth ≤2200 cm·day, pregnant fawns ($\bar{x}$ = 39.2 kg) were heavier (one-tailed test, t = 2.66, df = 32, P < 0.01) than non-pregnant fawns ($\bar{x}$ = 35.0 kg).

FETAL DEVELOPMENT

Fawn Does

The linear relationship between fetal length and time (Fig. 5) was highly significant (r^2 = 0.90, F = 157.94, df = 1,16, P < 0.001) for fawn does. Observations from 13 singleton and 5 twin (1 observation for 1 set of twins) fetuses were available for analysis. A serious outlier (date = 127, length = 57 mm) was estimated to have been 56 days of age, conceived on 10 January, and would have been 63 mm long on a date of 129.

Forehead-rump length increased with date (r^2 = 0.85, F = 38.63, df = 1,7, P < 0.001) for the data set modified on the basis of the estimated earliest and latest conceived fetuses (Fig. 6). Although the methodology for growth rate estimation included the latest conceived fetus, this fetus was deleted for this analysis because it was <63 mm and likely in curvilinear growth. This linear regression or Manitoba growth function (LENGTH = 2.671 DATE - 161.7, LENGTH represents forehead-rump length and DATE represents the number of days since the beginning of November, SE_{B_1} = 0.430) predicted a

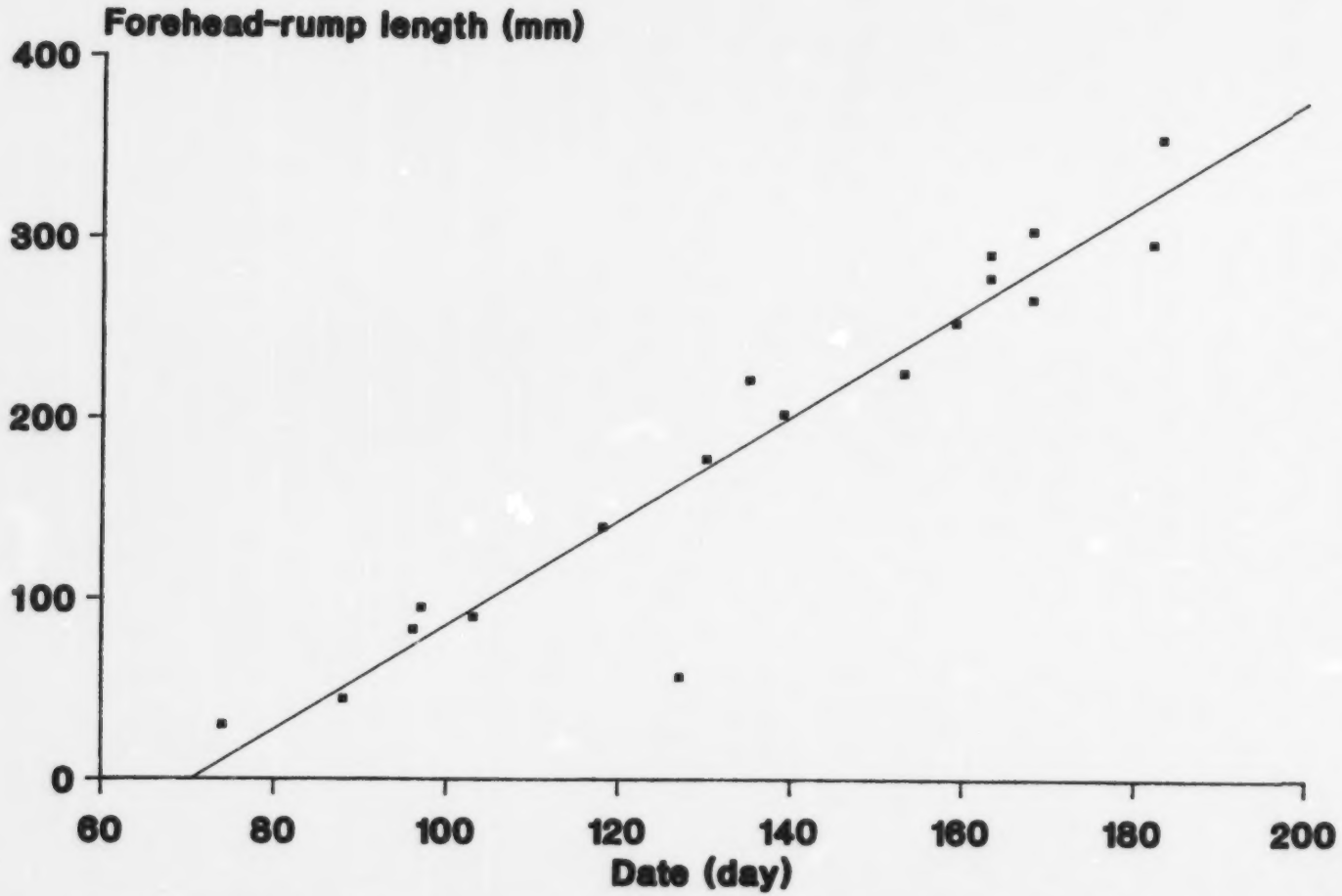

Fig. 5. Fetal growth in fawn white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Linear growth (forehead-rump length, mm) regressed against number of days between the beginning of November and date of collection. All data available for analysis utilized. Regression line significant at $P < 0.001$.

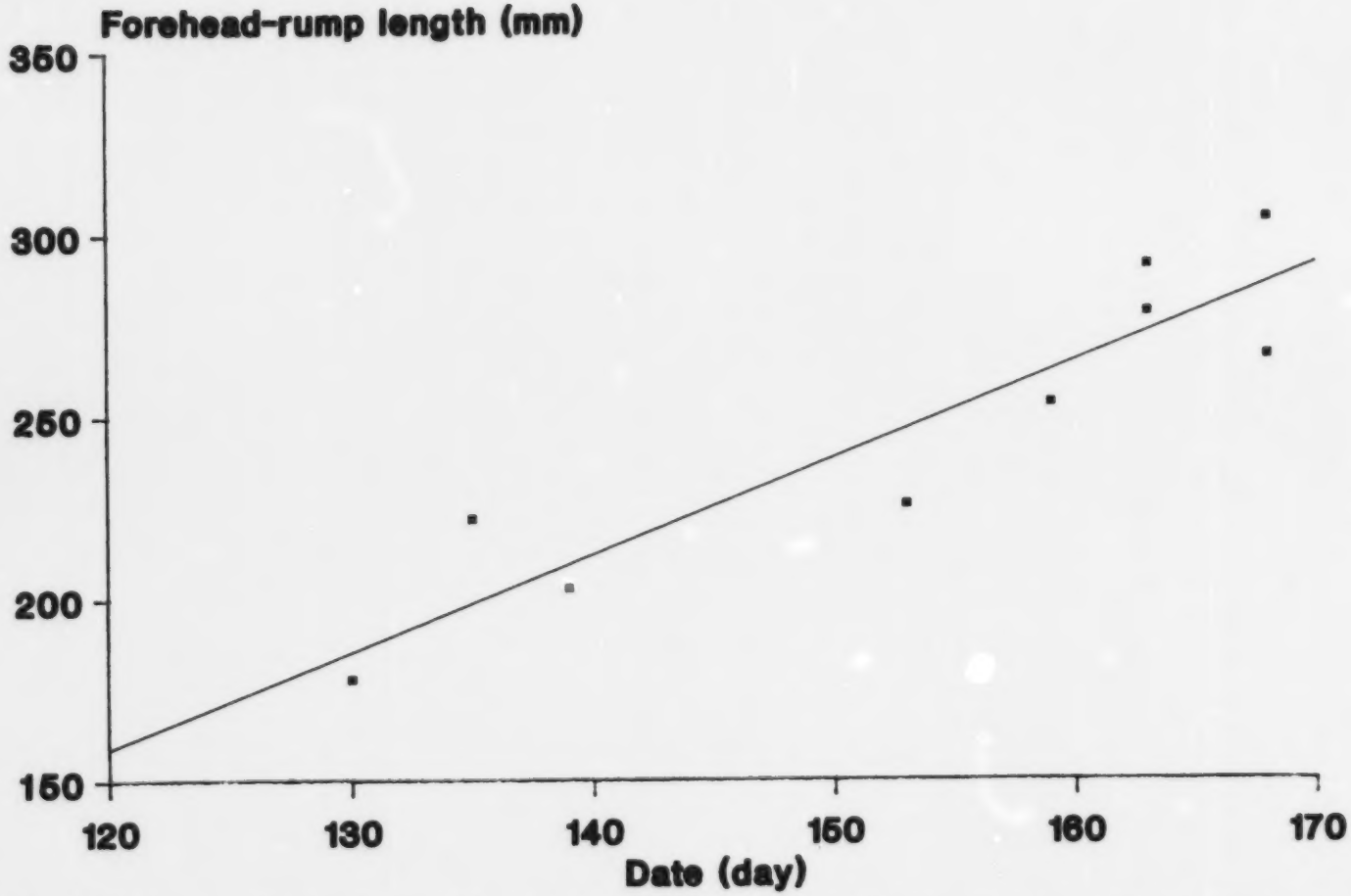

Fig. 6. Fetal growth in fawn white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Linear growth (forehead-rump length, mm) regressed against number of days between the beginning of November and date of collection. Data set modified to minimize bias for growth rate estimation. Regression line significant at $P < 0.001$.

fetal length of 63 mm on a date of 84. If such a fetus were 58 days old (i.e., the predicted age from Short 1970), the estimated mean conception date was 26 November (84 - 58). With Short's growth function, the estimated mean conception date was 12 December for this group.

For a fetus of length 380 mm, the Manitoba growth function predicted an age of 177 days (date - mean conception date) versus 150 days with Short's growth function. The estimated mean conception date from the Manitoba growth function suggested a fetal age of 133 days on 8 April and 150 days on 25 April. Addition of the estimated mean conception date (26.12) to Short's growth function (AGE = 0.29 LENGTH + 39.72) resulted in a form like the Manitoba function (DATE = 0.29 LENGTH + 65.84 or LENGTH = 3.448 DATE - 227). The slope of the Manitoba function did not differ from 3.448 (two-tailed test, H_o: $B_1 = 3.448$, $t = -1.93$, $df = 7$, $P < 0.10$).

The 2 fetuses from the greatest dates exhibited considerable size variation (298 mm at date = 182, 356 mm at date = 183) and were estimated to have been conceived 22 days apart. The small fetus was from a relatively snow-free winter (cumulative snow depth = 2189 cm·day) and the large fetus from a winter with considerably more snow (cumulative snow depth = 4675 cm·day).

Adult Does

When one twin was male and the other female, the male was longest in 7 sets, the female longest in 6 sets, no difference existed in 5 sets, and the slope of the growth function was not related to sex ($F = 0.31$, $df = 1,32$, $P > 0.20$). Little disparity existed between small siblings but substantial disparity could exist when siblings were large (eg., the latest collected twins differed by 87, 98, and 57 mm with the male sibling larger in the first 2 sets).

For twins where both siblings were the same sex, the slope of the growth function did not differ between males and females ($F = 0.02$, $df = 1,34$, $P > 0.25$). Similarly, slopes of regression lines for singletons, twins, and triplets did not differ (H_o: $B_{1(\text{singleton})} = B_{1(\text{twin})} = B_{1(\text{triplet})}$, $F = 0.13$, $df = 2,109$, $P > 0.25$) for a sample of 7 singletons, 84 twins (46 does), and 22 triplets (10 does). One or more of the siblings were often damaged and could not be measured. Forehead-rump length varied between 113 and 356 mm for singletons, 60 and 450 mm for twins, and 74 and 381 mm for triplets. Additionally, the

linear regression equations resulted from data sets which included 26 twins, 3 triplets, and 1 singleton >322 mm in length, and 10 twins and 1 triplet >380 mm in length.

Siblings often differed by ≈ 10 mm in length and sometimes differed considerably when large (Table 5). Several siblings were >380 mm long while 1 observation (forehead-rump length = 237 mm) was almost certainly incorrect (Table 5). With the exception of the questionable observation, the twins exhibiting the greatest difference had 1 sibling >380 mm long and the doe had a low visual femur fat of 55%. The twins which exhibited the least disparity (Table 5) originated from does with visual femur fat of >85% and 90% with one of the siblings >322 mm but <380 mm long. The triplets with the largest sibling <322 mm long included only 1 small sibling and were from a doe with a low visual femur fat of 40%. The visual femur fat of the other doe with triplets was extremely low and she had 1 large fetus and 2 very small fetuses.

For twins ≤322 mm in length (Fig. 7), the mean estimated conception date ($t = -0.69$, $df = 56$, $P > 0.30$) and variance (one-tailed test, $F = 1.46$, $df = 28,28$, $0.10 < P < 0.25$) did not differ between the smallest 29 ($\bar{x} = 22.3$) and largest 29 ($\bar{x} = 20.0$) fetuses. The middle observations were excluded for analysis because they were identical in size. Variance differed (one-tailed test, $F = 2.71$, $df = 44,14$, $P < 0.025$) between the smallest 15 and largest 45 fetuses; however, the mean estimated conception date ($\bar{x} = 20.7$ and $\bar{x} = 20.9$ respectively) did not (one-tailed test, $t = 0.06$, $df = 43$, $P > 0.90$). The estimated conception date was not related to fetal length ($r^2 = 0.01$, $F = 0.01$, $df = 1,58$, $P > 0.05$).

The estimated conception date varied between 5 and 40 for singletons, 4 and 44 for twins, and 15 and 46 for triplets when fetuses >380 mm long and those whose doe was in poor condition were deleted for analysis. Modification of the data set to minimize sampling bias resulted in a sample with dates of collection between 98 and 155 for singletons, 102 and 154 for twins, and 104 and 165 for triplets. To further minimize sampling bias, only data from singletons, twins, and triplets whose date of collection was between 102 and 154 were used for analysis. For twins (Fig. 8), forehead-rump length increased with date ($r^2 = 0.68$, $F = 93.69$, $df = 1,45$, $P < 0.001$) and the slope of the regression line (4.135) did not differ from 3.448 ($t = 1.61$, $df = 45$, $P \approx 0.10$). With the addition of singletons and triplets to the data set, forehead-rump length increased with date ($r^2 = 0.67$, $F = 119.76$, $df = 1,60$,

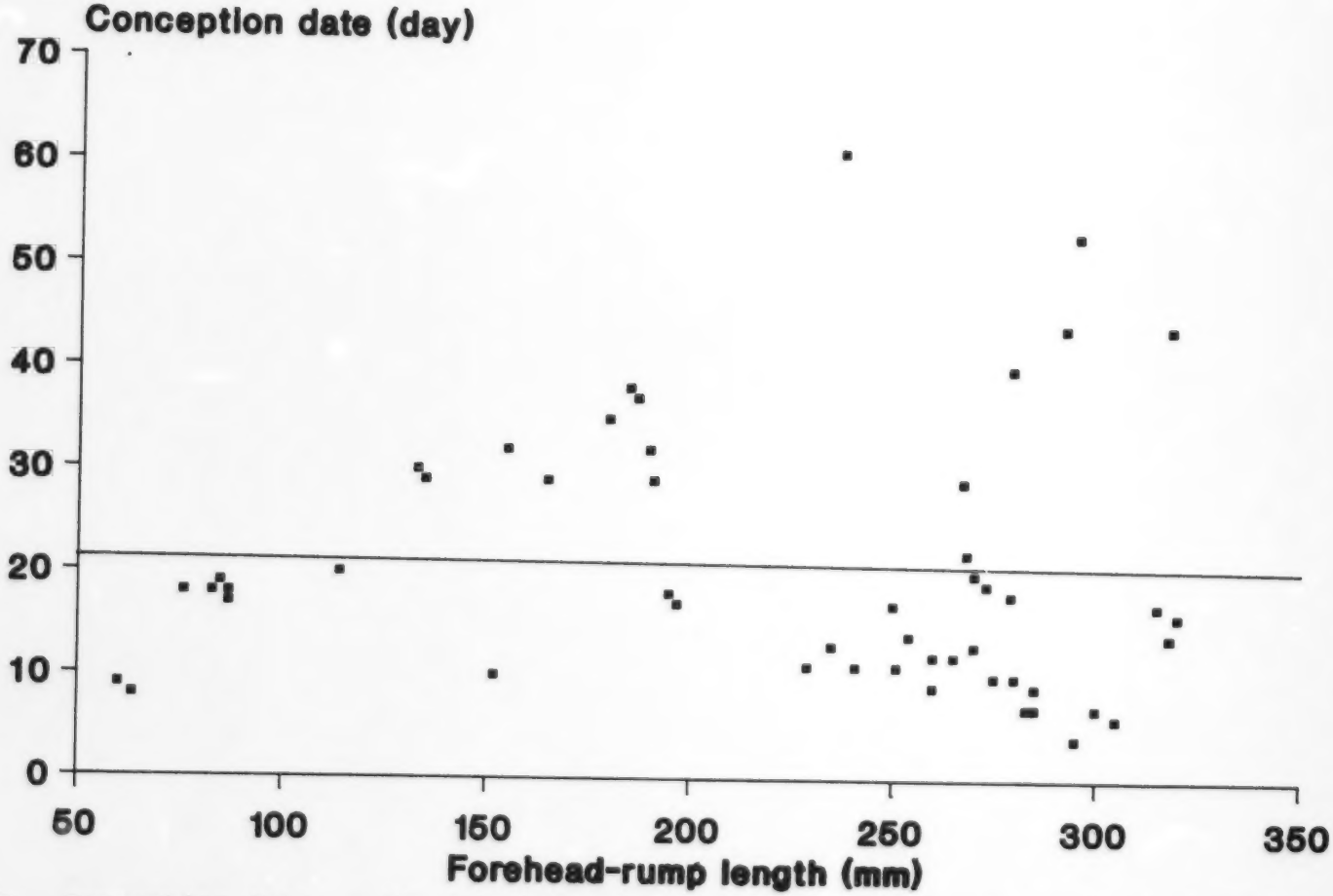

Fig. 7. Conception date, estimated from size, vs. size (forehead-rump length, mm) for twin fetuses ≤322 mm long from adult white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Conception date defined as the number of days beyond the beginning of November. Regression line not significant at $P < 0.05$.

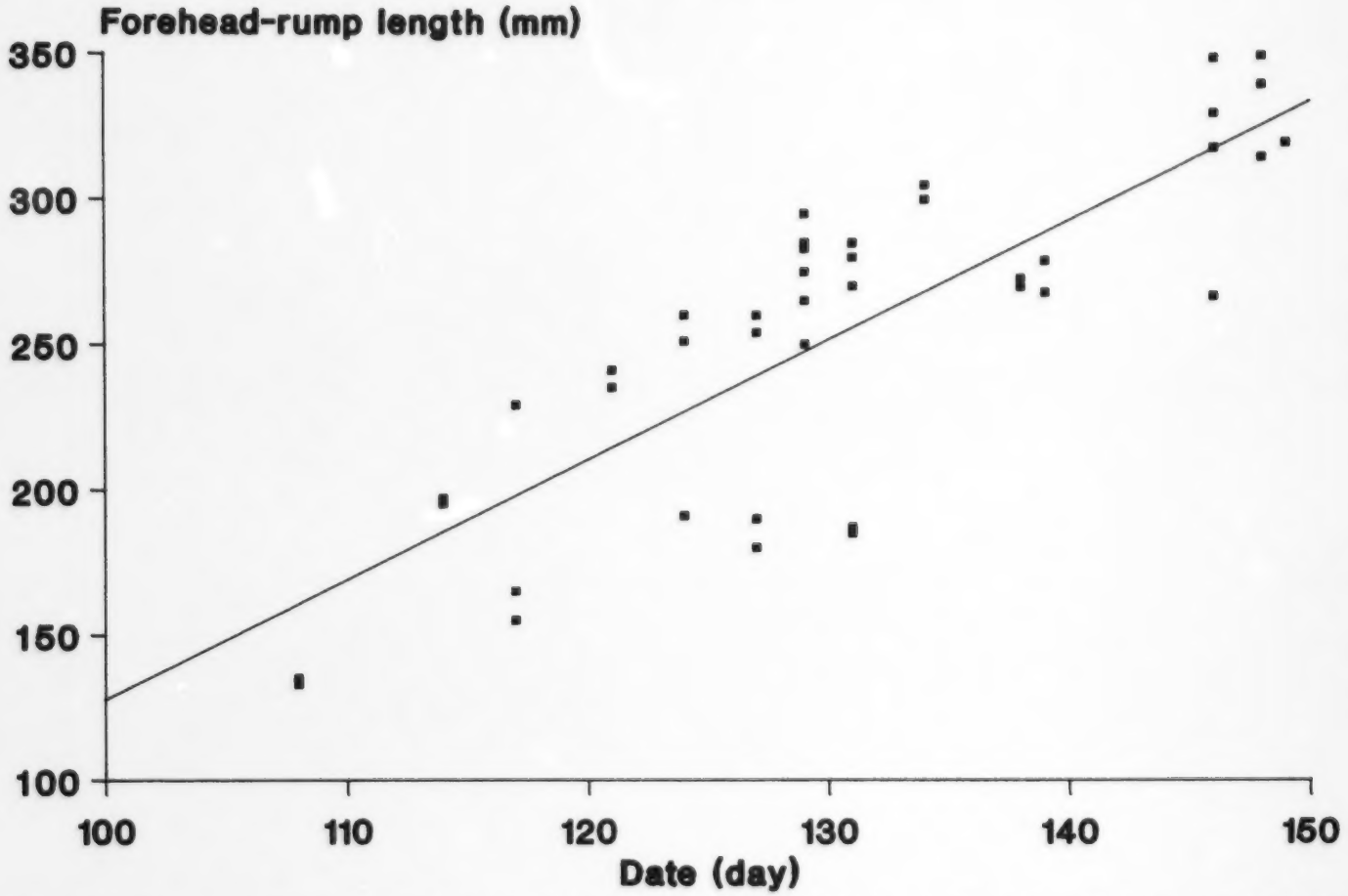

Fig. 8. Growth of twin fetuses from adult white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Linear growth (forehead-rump length, mm) regressed against number of days between the beginning of November and date of collection. Data set modified to minimize bias for growth rate estimation. Regression line significant at $P < 0.001$.

$P < 0.001$) and the slope of the regression line (4.419) differed from 3.448 ($t = 2.40$, $df = 60$, $P < 0.02$).

Table 5. Twin and triplet siblings which differed substantially in forehead-rump length (mm). Age difference (days, estimated with growth function of Short (1970)) and visual femur fat (%) of the doe for white-tailed deer from southwestern Manitoba.

Forehead-rump length	Size difference	Estimated age difference	Visual femur fat
349.3 317.5	31.8	9.2	>85
323.9 237.0[a]	86.9	25.2	85
275.0 250.0	25.0	7.3	90
393.0 295.0	98.0	28.4	55
375.0 318.0	57.0	16.5	55
300.0 300.0 200.0	100.0	29.0	40
381.0 152.0[b] 152.0[b]	229.0	66.4	1

[a]Forehead-rump length was likely wrong because fetus was almost as heavy as sibling (1127 versus 1237 g).
[b]Growth of fetuses appeared to have been impacted by doe condition.

Use of mean length from each set of twins, as opposed to use of length from each sibling, resulted in a slope (4.031) which did not differ from 3.448 ($t = 1.00$, $df = 23$, $P > 0.30$). The mean estimated conception date from this growth function (LENGTH = 4.031 DATE - 271.0) was 25 November versus 17 November from Short's growth function. The slope of the regression line (4.160) was not different from 3.448 ($t = 1.37$, $df = 25$, $P < 0.20$) with data from singletons included in the analysis. With the inclusion of mean

forehead-rump length from triplets, the linear regression equation was significant (r^2 = 0.72, F = 77.29, df = 1,30, P < 0.001) and the slope (4.436) did not differ from 3.448 (t = 1.99, df = 30, P > 0.05).

Forehead-rump length was regressed against date, visual femur fat of the doe, cumulative snow depth, cumulative minimum daily temperature, and number of days since snowmelt in a multiple linear regression analysis. Mean fetal length was utilized for twins and triplets to weight each observation equally (i.e., only 1 observation per doe) and fetuses were between 62 and 440 mm long. Both date (t = 15.68, df = 56, P < 0.01) and cumulative snow depth (t = -2.12, df = 56, P < 0.05) influenced forehead-rump length (R^2 = 0.85, F = 162.65, df = 2,56, P < 0.001). Cumulative snow depth and cumulative daily temperature were strongly correlated (r = -0.89, t = -14.66, df = 57, P < 0.01) for this data set.

For twins collected between dates 102 and 154, a multiple linear regression of mean fetal length versus date and cumulative snow depth (LENGTH = 4.723 DATE - 0.012 SNOW - 336.5) was significant (R^2 = 0.74, F = 31.34, df = 2,22, P < 0.001). Forehead-rump length varied with date (t = 7.67, df = 22, P < 0.01) and cumulative snow depth (t = 2.22, df = 22, P < 0.05).

Yearling Does

The male was heavier in 6 of 8 sets and longer in 7 of 8 sets of twins where 1 sibling was male and the other female. Siblings were the same length in 4 sets of these twins. The slopes of the relationship between forehead-rump length and date did not differ between sexes (F = 0.27, df = 1,18, P > 0.25). Growth rates of singletons and triplets were not compared to that of twins due to small sample sizes.

The mean forehead-rump length was used for twins and conception was estimated to have occurred between dates 3 and 49 for singletons and twins. Following adjustment of the data set to minimize sampling bias, observations between collection dates of 107 and 153 were used to estimate fetal growth rate. Forehead-rump length increased with date (Fig. 9, F = 14.87, df = 1,10, P < 0.005); however, the relationship was weak (r^2 = 0.60) compared to those for fawns and adults. The slope of the linear growth function (LENGTH = 3.123 DATE - 183.5) was not different from 3.448 (t = 0.40, df = 10, P > 0.20). Several observations from the winter of 1982-83 exhibited a substantial

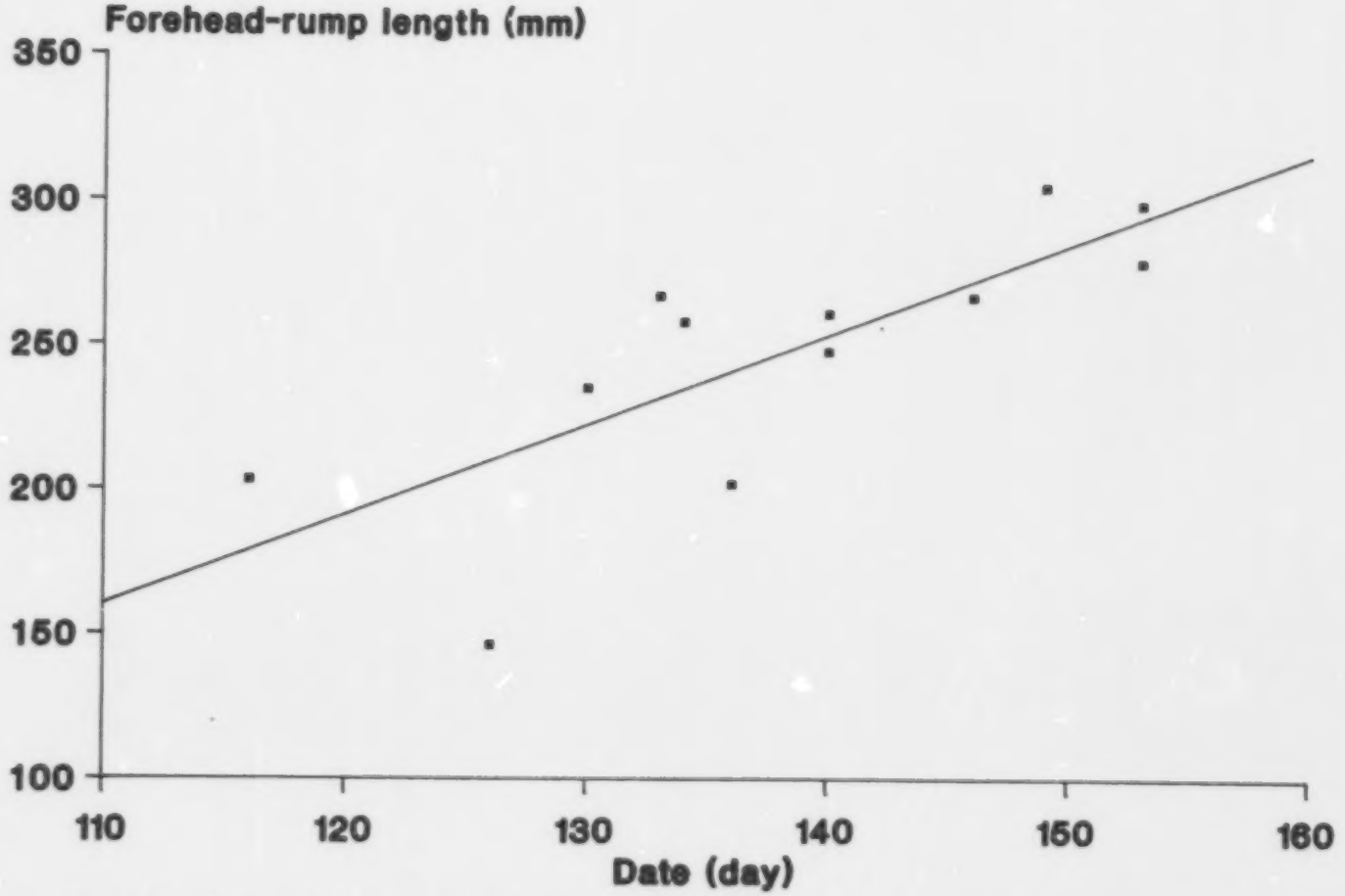

Fig. 9. Growth of singleton and twin fetuses from yearling white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85. Linear growth (forehead-rump length, mm) regressed against number of days between the beginning of November and date of collection. Data set examined to minimize bias for growth rate estimation. Regression line significant at $P < 0.005$.

difference in forehead-rump length between siblings (i.e., 245, 270 mm and 285, 325 mm). Additionally, the observations from the greatest date were from does with twins and visual femur fat estimates of 1% and 40%. The mean estimated conception date was 21 November with the growth function versus 27 November from Short's growth function. The growth rate of fetuses from yearling does was not different from that of twin fetuses from adult does (B_1 = 4.031, F = 0.84, df = 1,32, P > 0.37) or all fetuses from adult does (B_1 = 4.436, F = 1.89, df = 1,39, P > 0.17) when heterogenous variance was assumed.

For a larger data set of fetuses between 146 and 364 mm long, forehead-rump length (mean for twins) was regressed against date, visual femur fat of the doe, cumulative snow depth, cumulative minimum temperature, and number of days since snowmelt in a multiple linear regression (backwards elimination) analysis. The longest observation resulted from twins with forehead-rump lengths of 352 and 375 mm. Forehead-rump length varied with date (t = 4.17, df = 15, P < 0.01) but not cumulative snow depth (P > 0.20) for this small data set.

Weight-Length Relationships

The relationship between weight and forehead-rump length for fetuses from adult does was investigated for fetuses up to 2670 g in weight, 445 mm in length, and which had died up to a date of 205. The datum which was obviously erroneous (twins with the male 324 mm, 1237 g and the female 237 mm, 1127 g) was not included in analyses. The data best fit the power model for male (r^2 = 0.97, F = 985.60, df = 1,26, P < 0.001) and female (r^2 = 0.98, F = 838.60, df = 1,20, P < 0.001) fetuses. The relationship between weight (WT) and length was $WT = 0.000085\ LENGTH^{2.798}$ ($\ln WT = 2.798\ \ln LENGTH - 9.365$) for males and $WT = 0.000164\ LENGTH^{2.643}$ ($\ln WT = 2.643\ \ln LENGTH - 8.716$) for females. The slope of the ln (natural logarithm) transformed linear relationships did not differ between the sexes (F = 1.42, df = 1,46, P < 0.24). On this basis, observations where fetal sex was unknown were added to the data set. This data fit the power model (Fig. 10, r^2 = 0.97, F = 1712.60, df = 1,52, P < 0.001) described by $WT = 0.000109\ LENGTH^{2.736}$ ($\ln WT = 2.736\ \ln LENGTH - 9.124$).

Analysis of fetuses <322 mm long produced rates of increase which did not differ (F = 1.77, df = 1,37, P < 0.19) between males (2.756) and females (2.559). For the data set which combined males and females ≤322 mm long, weight and length best fit the power model (r^2 = 0.96, F = 1111.60, df = 1,41,

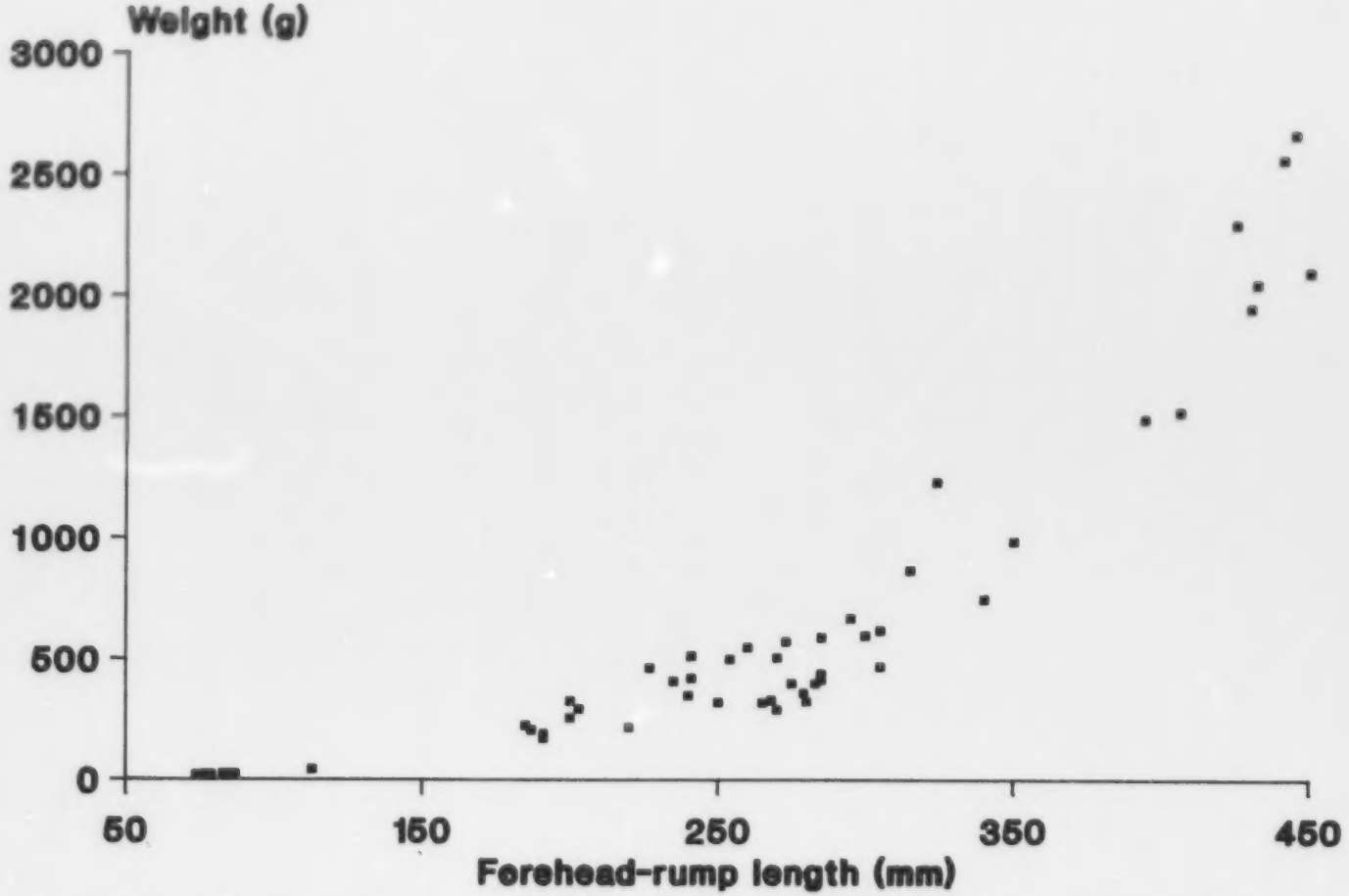

Fig. 10. Weight (g) vs. length (forehead-rump, mm) of fetuses from adult white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85.

$P < 0.001$) and the relationship was described by $WT = 0.000196\ LENGTH^{2.619}$ ($lnWT = 2.619\ lnLENGTH - 8.537$).

For fetuses from yearling does, males and females were analyzed together due to small sample sizes (i.e., 9 males, 7 females, and 1 unknown). The data best fit the power model (Fig. 11, $r^2 = 0.93$, $F = 193.00$, $df = 1,15$, $P < 0.001$); however, it also fit other models well (eg., $r^2 = 0.86$ for the linear model). The model which resulted ($WT = 0.000157\ LENGTH^{2.677}$) is very tentative due to the small sample size and lack of data from larger fetuses.

As the longest fetus from a yearling doe had a forehead-rump length of 375 mm, only fetuses ≤375 mm in length were used to compare fetal growth from adults and yearlings. The rate of increase did not differ ($F = 0.01$, $df = 1,60$, $P > 0.25$) between adults ($WT = 0.000166\ LENGTH^{2.667}$, $P < 0.001$) and yearlings ($WT = 0.000166\ LENGTH^{2.667}$, $P < 0.001$). For the data set which combined observations from yearlings and adults, the power model (Fig. 12, $r^2 = 0.97$, $F = 2101.00$, $df = 1,69$, $P < 0.001$) was described by $WT = 0.000111\ LENGTH^{2.734}$ ($lnWT = 2.734\ lnLENGTH - 9.106$). Exclusion of fetuses >322 mm long resulted in the relationship ($r^2 = 0.98$, $F = 1376.00$, $df = 1,55$, $P < 0.001$) described by $WT = 0.000174\ LENGTH^{2.647}$ or $lnWT = 2.647\ lnLENGTH - 8.656$.

DISCUSSION

REPRODUCTIVE PERFORMANCE

The pregnancy rate of fawns from southwestern Manitoba was similar to those found by Ransom (1964) in the Turtle Mountain and Duck Mountain areas. A similar pregnancy rate found for fawns collected in January versus February indicates that potential late pregnancies (eg., estimated conception dates of 10 January in this study and 3-20 March by Kerr and Peterson 1988) did not seriously influence rate estimates (i.e., Ransom (1964) used fawns collected in February or later). The fetal rate of 1.12 fetuses per pregnant fawn was also similar to those found by Ransom (1964) in the Turtle Mountain and Duck Mountain areas.

The pregnancy rate of adult does from southwestern Manitoba was almost identical to that found by Ransom (1964) for adult does from diverse areas of Manitoba. The non-pregnant adults were relatively old (i.e., 6.5-8.5 and 12.5 years old). Similarly, no difference in pregnancy rate could be detected between yearling does from southwestern Manitoba and those examined by Ransom

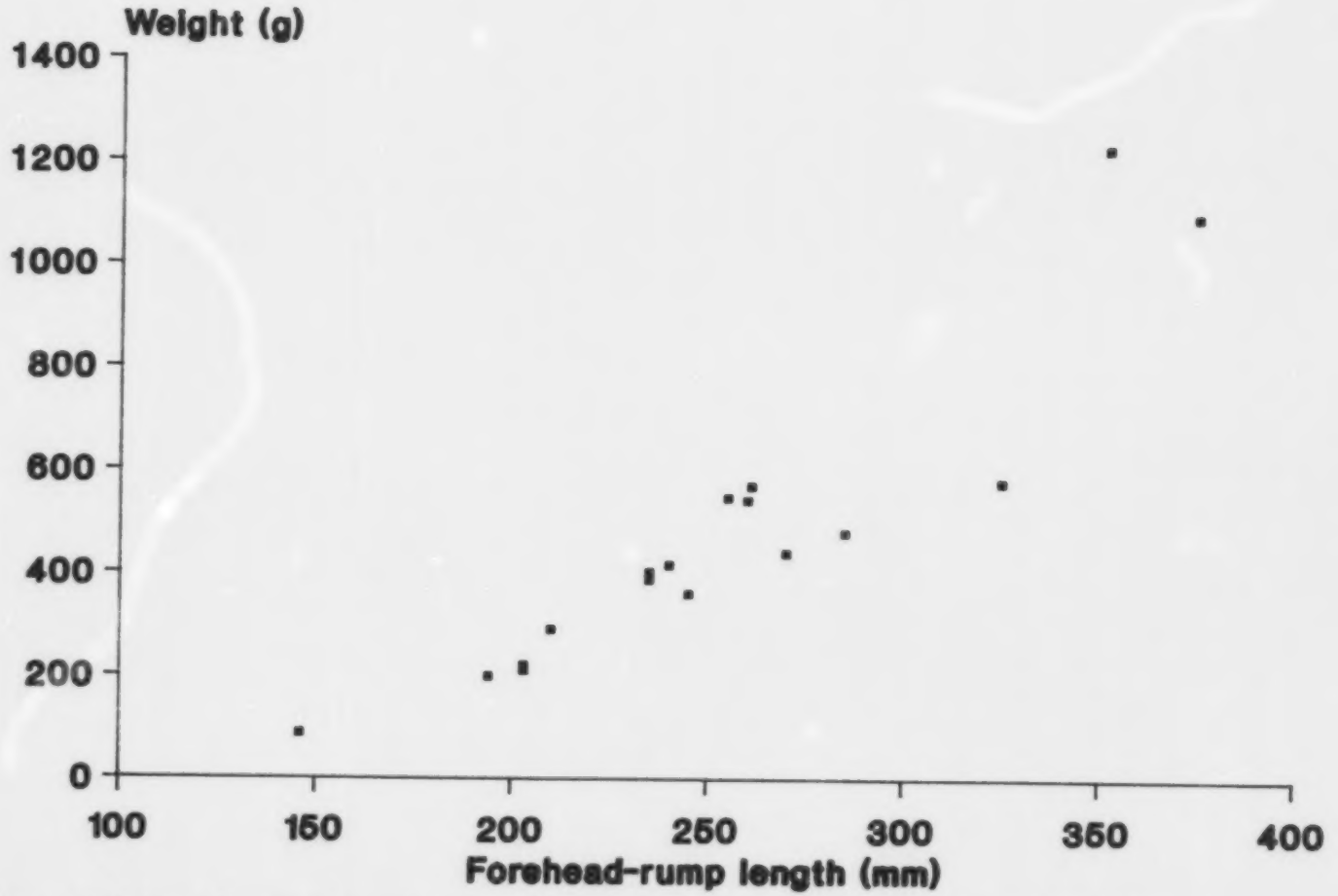

Fig. 11. Weight (g) vs. length (forehead-rump, mm) of fetuses from yearling white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85.

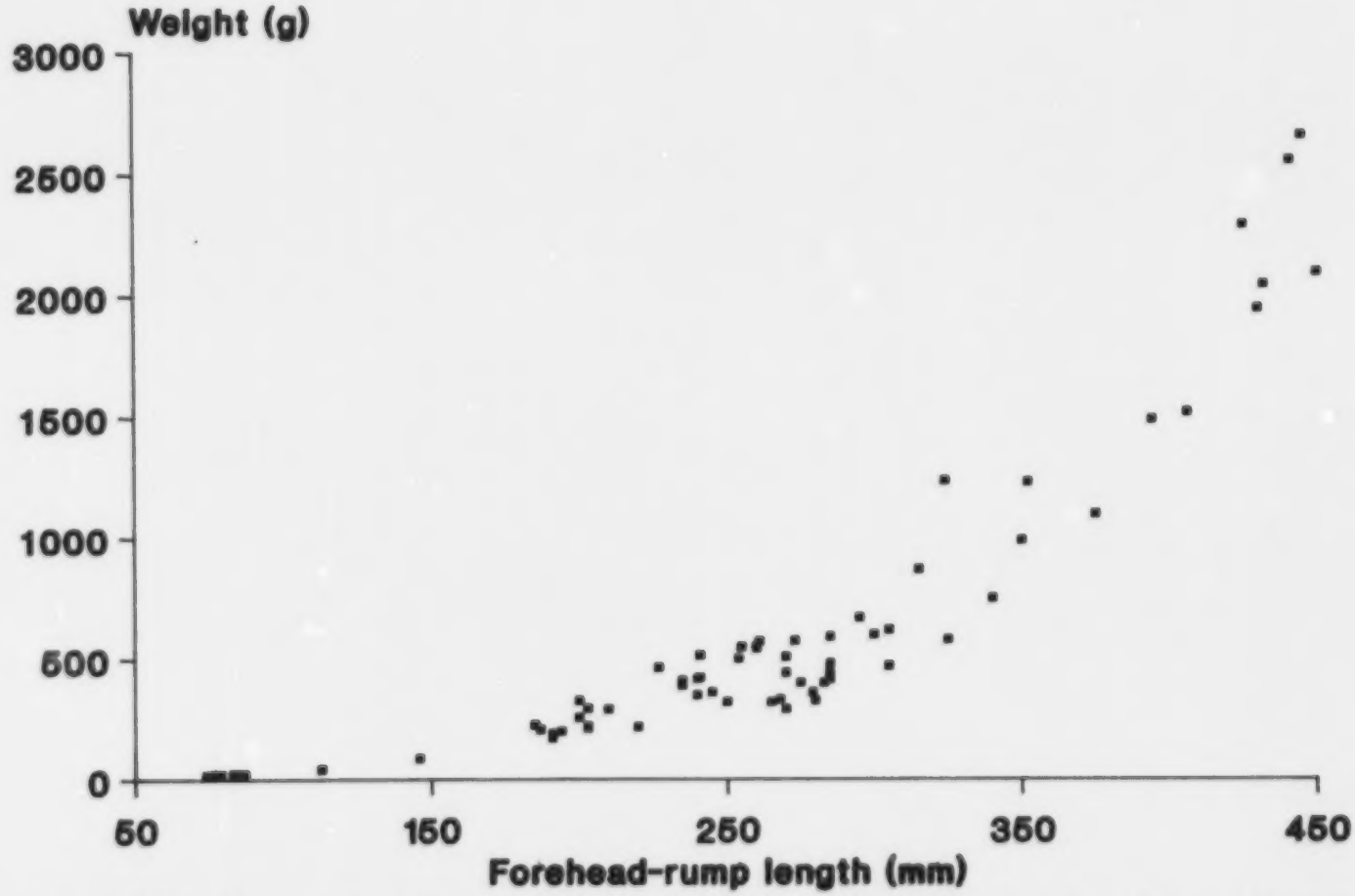

Fig. 12. Weight (g) vs. length (forehead-rump, mm) of fetuses from yearling and adult white-tailed deer from southwestern Manitoba, 1976-77 to 1984-85.

(1967) for the Turtle Mountain, Duck Mountain, and Whiteshell areas.

In contrast to Ransom (1967), the pregnancy rate of yearlings from southwestern Manitoba was lower than that of adult does. Unfortunately, this result is somewhat questionable because 3 yearling does were indicated as having been "not pregnant" but with "uterus enlarged, no fetuses present" (Chranowski 1984a) suggesting that they may have been recent pregnancies. As the appearance of a uterus is unchanged until ≈ 20 days gestation (Cheatum and Morton 1946) and a fetus would be ≈ 0.3 cm long by this age (Soprovich In press), careful examination of the uteri should have revealed a fetus if one was present. At the same time, given the conception dates estimated by Ransom (1966) for the Turtle Mountain area, these does had died early enough (1 on 8 January, 2 on 23 January) that they may have had recent pregnancies. The pregnancy rate of yearling does, although estimated to be lower than that of adults, was not statistically different with these observations deleted. Although it appears that yearlings have a lower rate of pregnancy than adult does, more data are required to definitively resolve this question. Adult does from southwestern Manitoba, like those from several areas of Manitoba (Ransom 1964), had a greater fetal rate than did yearlings.

The fetal rate of adult does from southwestern Manitoba was not different from that found by Ransom (1964) for the Turtle Mountain area. Unlike Ransom (1964) who suggested the fetal rate to have been greater in 1961 than 1962, temporal variation was not found for adults from southwestern Manitoba. The different conclusion relative to temporal variation may result from the annual samples available for this study often having been small, the 1962 rate having been an infrequent occurrence, or the lack of control over potentially important independent variables in Ransom's analysis. Although the fetal rate of adult does found in this study was not statistically different from that found by Ransom (1964), its higher value supports Ransom's conclusion that the fetal rate of adult white-tailed deer was particularly low during 1962 and suggests that this was an infrequent event. Irrespective of the reason for the difference between Ransom's and this study, the inability to detect annual variation in fetal rate indicates that collection of such data from adult does will provide little practical information when sampling is conducted at the intensity of this study.

The fetal rate of yearling does from southwestern Manitoba did not differ from that found by Ransom (1964) for a small sample of yearlings from

the Turtle Mountain area. Although not possible to detect differences between annual fetal rates and Ransom's, fetal rate appeared to vary temporally for yearling does from southwestern Manitoba. The apparent temporal variation in fetal rate among yearling does, but not adult does, provides support for the suggestion that yearlings are the most sensitive environmental indicators (Ransom 1967). For the examination of temporal variation in fetal rate, distributions were not normal (i.e., 14 singletons, 24 sets of twins, 1 set of triplets), sampling was likely not random (i.e., deer originated from different areas in different years), and sample size was small (<20) and varied considerably between years, all violations of the assumptions requisite to use of ANOVA (Kleinbaum and Kupper 1978). Although ANOVA is robust relative to the assumption of normality and homogeneity of variance for designs with equal sample sizes (Glass et al. 1971), given the small and variable annual sample sizes in this study, temporal variation in the fetal rate of yearling does from southwestern Manitoba can only be suggested. Additionally, multiple comparison of annual rates via t test (eg., 1980-81 to 1982-83) will result in 1 of 20 "significant" results by chance alone ($P \leq 0.05$), therefore such results must also be treated cautiously.

The comparison of data from this study and Ransom (1964) was made subject to the recognition that the deer originated from somewhat different geographic areas. Secondly, while Ransom (1964) may have followed a sampling regime designed to provide a random sample, it appears that the deer sampled in this study were also representative given that the fetal rate of adult does did not differ between studies (i.e., does in very poor condition and potentially with fewer fetuses were not the only does sampled in this study). Annual variation in sampling intensity was such that fetal rate estimates for fawns, yearlings, and adults could have been biased if fetal rate varied temporally, as suggested for yearlings (this study) and adults (Ransom 1964, Verme 1977). Additionally, it must be recognized that Ransom's (1964, 1967) conclusions were based on analyses which did not fully control the independent variables and should be considered somewhat tentative. Finally, because substantial neonatal mortality can occur as related to doe condition and fawn weight at birth (Verme 1962, Verme 1963), changes in gross productivity within the bounds which occur in Manitoba are inconsequential relative to population change and herd structure. It is most important to understand how the environment impacts net productivity, and of almost no importance to document

small annual changes in gross productivity, for the purpose of understanding and influencing white-tailed deer population dynamics.

CONDITION, BODY WEIGHT, AND PREGNANCY IN FAWNS

Fawn condition, as measured by the visual femur fat index (VFF), was not shown to be influenced by pregnancy. Although femur fat (chemical determination) and total body fat (TBF) are related linearly below ≈ 6% TBF in mule deer (Odocoileus hemionus) fawns (Torbit et al. 1988), the index used in this study was very crude as evidenced by a poor linear relationship between VFF and FF (chemical determination) for fawns (D. W. Soprovich, unpubl. data). Given the available sample sizes, the reasonably low value of alpha (P ≈ 0.15), the weakness of the index to fawn condition, and the non-linear relationship between VFF and cumulative snow depth (D. W. Soprovich, unpubl. data), it is quite possible that large samples would indicate the influence of pregnancy on fawn condition.

The ability to ovulate is closely related to body composition (% TBF) in humans (Frish 1980) and it is likely that this condition applies to mammals generally. Under conditions of substantial resource limitation, body condition has been shown to influence the ability of adult red deer (Cervus elaphus) hinds to breed (Clutton-Brock 1985). Similarly, it is likely that white-tailed deer fawns must achieve a minimum condition (% TBF) to allow ovulation and subsequent pregnancy. Otherwise, such a physiological miscue could frequently result in death of the female due to the additional protein and energetic cost of pregnancy. Cothran et al. (1987) provide data which suggests that, for a given date, white-tailed deer which conceive early or at an average date are in better condition than non-pregnant does (comparison of Fig. 1a and 2 in Cothran et al. 1987). Additionally, does which conceived late appeared to be in better condition than lactating non-pregnant does and in ≈ the same condition as non-lactating non-pregnant does. Utilization of this conceptual framework for ovulation, and subsequent fertilization, suggests that pregnant fawns would be in better condition than non-pregnant fawns at the date of conception. The impact of pregnancy on fat depletion is somewhat more complex however. For fawns of equal size (bone structure, protein mass), pregnancy would exert an additional energetic cost (Oftedal 1985) such that the rate of fat depletion should exceed that of non-pregnant fawns. At the same time, benefits relative to size might serve to offset the

cost of pregnancy (eg., Parker et. al. (1984) indicate that brisket height can influence the cost of locomotion) if pregnant fawns were larger.

Although not significantly different, VFF decreased at a quicker rate for non-pregnant fawns which is contrary to expectations based upon the increased cost of pregnancy. This likely results because the condition index is a poor measure of body condition. Even if pregnant fawns had proportionately more fat and they depleted their reserves at a faster rate than non-pregnant fawns, the change could be detected later in pregnant fawns if it took longer to reach a TBF at which VFF began to decline. Also contrary to expectations, pregnant and non-pregnant fawns did not differ initially (i.e., at zero cumulative snow depth) with respect to body condition, as measured by VFF. Rather than lack of a real difference in condition (i.e., TBF), this result likely reflects the fact that VFF does not measure difference at the upper end of the condition continuum (eg., for mule deer at relatively high TBF see Fig. 2, Torbit et al. 1988).

The relationship between weight and cumulative snow depth was investigated because this crude measure of condition might be an improvement over VFF. This approach ignores any effect which body size (i.e., due to physical maturity or genetics) might have on a fawns ability to become pregnant (i.e., it does not differentiate between small fawns in good condition and large fawns in poor condition, if this occurs). As anticipated, initial body weight was greater for pregnant fawns; however, the difference attributable to differences of body size versus body composition is unknown. Body weight decreased with cumulative snow depth for pregnant fawns but not at standard alpha levels for non-pregnant fawns ($P < 0.10$). As body weight would be low when fawns starve at high cumulative snow depth, the lack of statistical significance almost certainly reflects the great variation in body weight within the population (i.e., the crudeness of weight as a measure of condition) rather than lack of a relationship between weight or condition and cumulative snow depth. Lack of a relationship or the existence of a relationship with a relatively low rate of decrease for non-pregnant fawns is noteworthy because it suggests that increased weather severity due to excessive snow impacts non-pregnant fawns less than pregnant fawns. This conclusion is opposite to that when VFF was used as the measure of condition, and is consistent with the hypothesis that pregnancy increases the rate of fat depletion. Similarly, Cothran et al. (1987) observed that does (age $\geq$1.5

years) which conceived late were in relatively poor condition at conception (as hypothesized for non-pregnant fawns) and, unlike does which conceived early and on average, did not exhibit a decrease in estimated TBF with time (similar to pregnant versus non-pregnant fawns as related to snow conditions). With body weight as the index to condition, these results support both the conceptual framework and the findings of Cothran et al. (1987).

Body weight decreased with time for both pregnant and non-pregnant fawns. This suggests that changes in body weight could relate to the cumulative influence of several variables (eg., low temperature, elevated snow depth, poor food quality, decreased consumption rate). Similar to the examination of snow depth in isolation, snow-related weather severity had no impact on non-pregnant fawns but may have impacted pregnant fawns (no impact on pregnant fawns at standard alpha levels but larger samples might prove otherwise) when the influence of time was controlled.

The possibility that weather severity impacts pregnant and non-pregnant fawns differentially, as suggested in this study, may provide a good example of the dynamic force of natural selection. In years of mild winters, pregnant fawns may be able to survive the winter and successfully raise a viable offspring thereby contributing to their long-term fitness. In years of severe winters, it appears that survival may be influenced by pregnancy and that long-term fitness would be greater for the non-pregnant fawn which lives to reproduce in the future. In other words, in some years it might be advantageous to be pregnant while in others it might not. Interestingly, in an unpredictable environment, a net product of this model might be a population which exhibits long-term viability.

Unfortunately, these analyses are compromised in a number of respects. There were relatively few observations of pregnant fawns from winters with deep snow, hence relationships for pregnant fawns must be considered tentative. Body weight incorporates change which can occur in the protein mass (Torbit et al. 1985); therefore, the crudeness of weight as a measure of condition is exacerbated. The larger initial body weight and perhaps size of pregnant fawns, possibility of growth during some winters, threshold nature of the measure of snow-induced stress, potential for some animals to have access to supplemental feed, and the fact that fawns sampled early versus late are likely from different populations in the statistical sense (due to the death of less fit, possibly smaller fawns) all contribute to these analyses being

speculative. Additionally, because the proportion of pregnant fawns in annual samples varied and samples were small, the comparison of pregnant and non-pregnant fawns was also a comparison of different years and winters to some extent. Consequently, results of the analyses may have reflected differences between years (eg., annual variation in fawn lean body mass at the beginning of winter as related to summer range conditions). To properly examine the interaction between pregnancy, fitness, and winter weather for fawns, an ability to accurately predict body condition is required or, in the absence of such an ability, body weight combined with a measure of body size might prove adequate.

FETAL DEVELOPMENT

Estimation of Fetal Growth Rate

The method of fetal growth rate estimation developed by Soprovich (In press) requires several assumptions to be met for an accurate estimate to result. Fundamentally, bias results when sampling is extended too close to conception or parturition, and is sensitive to the width of the conception distribution. This method provides an unbiased estimate of growth rate if, for each date of death, fetuses from the complete range of conception dates can be included (i.e., bias will result if fetuses are excluded because they are in their curvilinear growth phase or, alternatively, all data are used but non-pregnant or post-partum does and fetuses in their curvilinear phase are sampled). A potential distribution of forehead-rump length about date of death illustrates the impact of the deletion of observations on estimated growth rate (Fig. 13). If only fetuses in their linear growth phase (i.e., ≥63 mm long according to Short 1970) are used for analysis, mean fetal length will be overestimated at dates in the vicinity of a true mean of 63 mm. Similarly, if fetuses >380 mm long and potentially in curvilinear growth (Short 1970) are excluded, mean fetal length will be underestimated at a true mean of 380 mm. The consequence of either of these data handling procedures is the underestimation of slope or growth rate. Similarly, when data are not excluded but sampling occurs near conception or parturition, growth rate will be biased as fetuses are missed or in curvilinear growth (Soprovich In press).

Fawn Does

The utilization of data on Manitoba fetuses to develop a growth

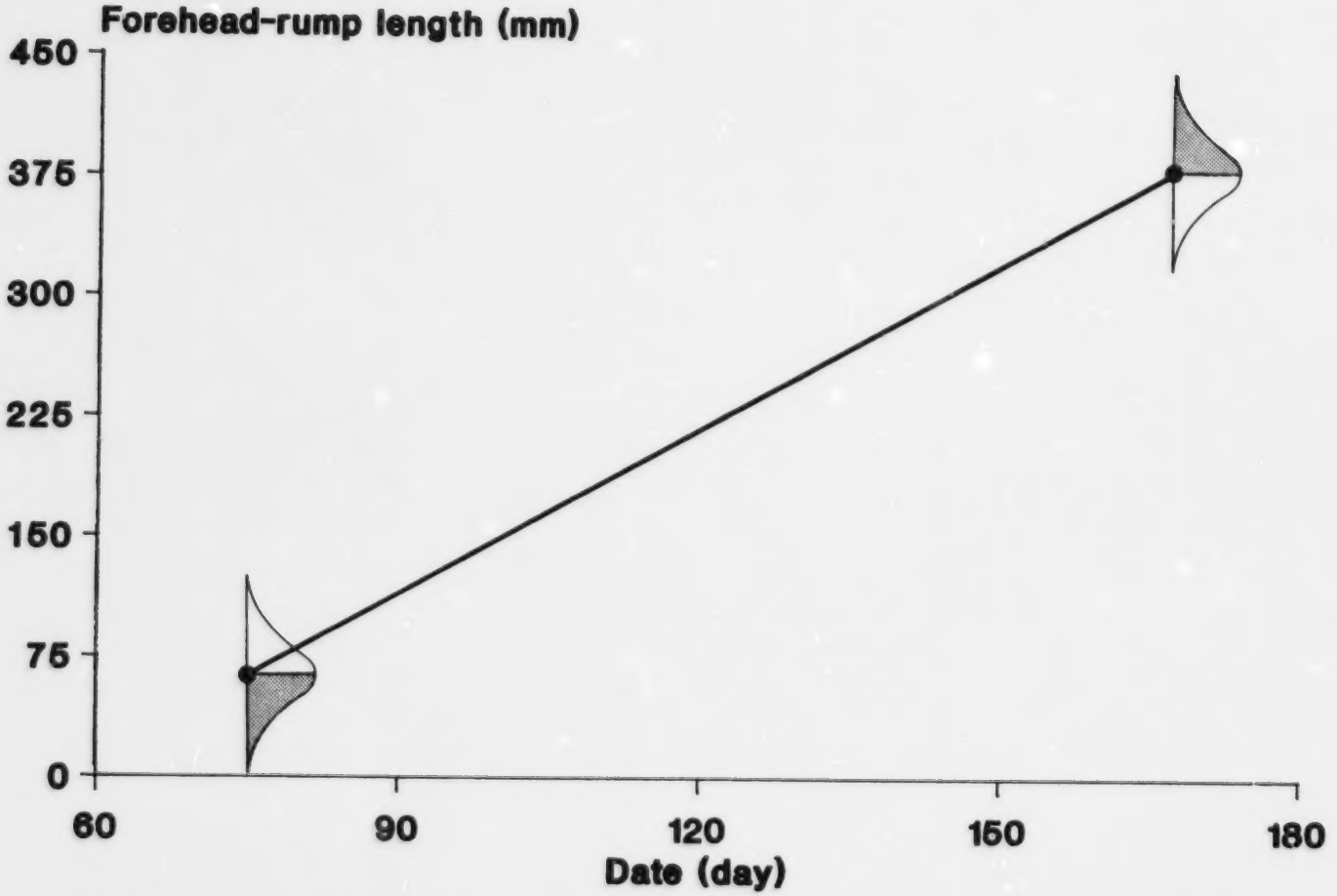

Fig. 13. Potential distributions of forehead-rump length (mm) about means of 63 mm (date = 75) and 380 mm (date = 172). Deletion of observations ≤63 mm long and/or ≥380 mm long (shaded areas of distributions) would result in overestimation (at 63 mm) and/or underestimation (at 380 mm) of the true mean and subsequent underestimation of growth rate.

function, and subsequent use of this function for predictive and comparative purposes, assumed that fetal growth to 58 days of age was the same as found by Short (1970). Although condition of the doe may affect forehead-rump length at fetal age >150 days and weight at fetal age >133 days for adult does (examination of data in Verme 1963), the same may not be true for fawns. Fawns may differ for a number of reasons, including the potential for age-related differences in body condition prior to the winter (eg., Johns et al. 1984 for does of unknown reproductive status, Torbit et al. 1988 for both sexes of mule deer fawns versus adult does) and the different manner in which their environment may influence energy dynamics (i.e., see Hobbs 1989 for mule deer). Additionally, Verme's (1963) data appears to demonstrate that doe condition impacted fetal growth of twin fetuses but not singletons.

The estimated linear growth rate of fetuses from Manitoba fawns, although of low precision, was considerably less than that of fetuses from Michigan adult does (Short 1970). Although the observed difference was not statistically significant ($0.05 < P < 0.10$), the alpha value was low given the small sample size. At the same time, it must be recognized that the growth rate reported by Short (1970), although precise ($r^2 = 0.99$), was also an estimate and that the analyses conducted in this study assumed this rate to be accurate. Additionally, Short (1970) estimated growth rate over a wide range of fetal age which almost certainly included fetuses in curvilinear growth (Soprovich In press). Consequently, growth rate during the linear phase was likely underestimated by Short (1970) such that a rate >3.448 mm/day would have been more appropriate for comparative purposes with Manitoba fawns. A number of the large fetuses originated from a winter with a high cumulative snow depth (1978-79) and the visual femur fat of the does (i.e., VFF of 50%, 35%, 25%, and 25%), although often a weak indicator of condition for fawns (D. W. Soprovich, unpubl. data), suggested that they were in poor condition. Additionally, the substantial size disparity of the set of twins in this group (forehead-rump lengths of 267 and 305 mm) suggested that development had been affected by doe condition. If this was true, the fetal growth rates, as estimates of rates for does with adequate resource availability, were biased towards underestimation. At the same time, estimates of conception date might have been improved for the same reason. As the sample of fetuses from Manitoba fawns was very small, it is apparent that erroneous growth rate estimation could result simply from combination of data from different years

with different mean conception dates and/or environmental influences. As fawns generally represent the majority of deaths due to starvation (Sauer and Severinghaus 1983, D. W. Soprovich, unpubl. data) and exhibit the highest mortality rate (Sauer and Severinghaus 1983, Nelson and Mech 1986) in a population, a slower observed rate of fetal growth might simply be a result of their different sensitivity to the environment. Certainly, fawn does have the capability to produce large offspring (Verme 1985). To examine the hypothesis that fetal growth rate is slower in Manitoba fawns than Michigan adult does, data should be collected specific to that purpose.

Contrary to previous studies in other areas (Cheatum and Morton 1946) and Manitoba (Ransom 1966), fawns generally conceived during ≈ the same period as adult does on the basis of the Manitoba growth function. Although the estimated mean conception date may have been biased due to the influence of the environment (eg., as Bartmann (1986) has shown can occur for mule deer), similar problems may have impacted the data of Cheatum and Morton (1946) and Ransom (1966). The mean conception date estimated from the Manitoba growth function suggested that an average fetus (i.e., exclusive of the fetus estimated to have been conceived on 10 January) would be 150 days old on 25 April, a date by which snow has generally disappeared from southwestern Manitoba. Again, the small sample size and method to estimate fetal growth rate dictate that these estimates are very imprecise and inference based on these estimates is highly speculative. If fetal weight is not affected to 150 days of age in Manitoba fawns, the adaptation of delayed conception (i.e., according to Short's function, Ransom 1966) might allow fawns to grow a fetus to a date by which environmental conditions do not impact doe condition and impair fetal development. Additionally, hormonal regulation might allow rapid growth of late-conceived fetuses (Verme 1985), particularly during the late stages of gestation.

Similarly, slower growth of the fetus, if indeed it exists, could also represent an adaptation to allow successful parturition and good post-natal survival of the fawn in that the doe must continue to obtain sufficient nutrition for herself and fetus during the spring when food quality may be low. The benefit a fawn gains by becoming pregnant (i.e., gene flow) carries a significant energy cost to the dam the following summer (Oftedal 1985) which could influence growth, survival, and subsequent reproductive performance of the doe. The environment should also constrain conception date and growth

rate to ensure that offspring are not born too late with little chance to survive. Some fawns in Manitoba conceive at a date (eg., estimated conception date of 10 January in this study, 3-9 January and 17-23 January in Ransom 1964) such that offspring might not survive the subsequent winter due to their late birth and potentially limited opportunity to develop.

If fetuses from fawns exhibit a slow rate of growth, past utilization of growth functions (eg., Cheatum and Morton 1946, Short 1970) to age fetuses would have resulted in erroneous estimates of fetal age. Similarly, erroneous estimates of age would have resulted if fetal growth had been impacted through the influence of the environment on doe condition. Such errors would result in overestimation of conception date and are potentially responsible for the generally late conception dates estimated for Manitoba fawns (eg., data in this study with Short 1970, Ransom 1964).

Adult Does

Hamilton et al. (1985) found that fetal forehead-rump length was influenced by sex and litter size when does 1.5 to 3.5 years of age were fed a high protein diet. In this study, linear fetal growth was not found to differ between the sexes for twins or between singletons, twins, and triplets. Samples of singletons and triplets were small (7 and 10 does respectively), growth rate estimates were imprecise due to the fact that fetal age was unknown, the range of lengths differed between litter sizes, fetuses from different years with potentially different mean conception dates were included for analysis, and fetuses apparently in the process of reabsorption (eg., triplets 381, 152, and 152 mm in length) were included for analysis in this study. Although Verme's (1963) data are unclear on the influence of nutrition on fetal growth (Soprovich In press), his conclusion that linear fetal growth can be influenced by doe nutrition at fetal age >150 days (forehead-rump length >380 mm from Short 1970) suggests that inclusion of fetuses >380 mm in length could have increased the variance of the growth rate estimate. This appears to have occurred as indicated by the result that linear growth was influenced by snow depth. Given the above and the small impact of sex and litter size in the controlled experiment of Hamilton et al. (1985), the inability to detect sex or litter effects in this study is not surprising.

Short (1970) developed her linear growth function from data which included 4 sets of twins and observations up to a fetal age by which growth

might have been impacted by poor nutrition. The suggestion that Short (1970) may have underestimated fetal growth rate during the linear phase is supported by Ozoga and Verme (1985) who estimated the linear growth rate to be 3.846 mm/day for a relatively narrow age range (76 to 137 days). Ozoga and Verme (1985) developed their relationship based on x-ray of live does which may have impacted their estimate, as suggested by their findings that forehead-rump length was the least reliable predictor of age among those examined and that precision was relatively poor (r^2 = 0.72 versus r^2 = 0.99 for Short 1970).

Although generally similar in length, substantial variation sometimes existed between siblings, particularly when the doe appeared to be in poor condition. Such variation was documented for fetuses <380 mm long which suggests that, contrary to Verme (1963), doe condition can influence linear growth at fetal age <150 days. Short (1970) used fetuses from does believed to have been in excellent condition by Verme (1963) who considered does to be in poor condition if internal fat reserves were not "appreciable" and femur fat (visual and other methods) was ≤50% (Verme 1977). Although the definition of excellent condition is unknown, the definition of poor condition crude, and the status of internal depots of deer from this study unknown, it appears that several does with variably-sized fetuses <380 mm were in poorer condition than those used by Short (1970). Substantial variation sometimes existed even for relatively small fetuses (eg., twins of 250 mm, 275 mm). Consequently, utilization of Short's or any linear growth function can result in considerable difference in the estimated age of each sibling. A standard method of estimating fetal age should be utilized under these circumstances (eg., length of largest fetus, mean length).

Fetal age influenced the conception distribution but not the mean conception date of twin fetuses ≤322 mm long. This result was different from that of Bartmann (1986) for mule deer; however, Bartmann (1986) used fetuses up to ≈ 400 mm long and concluded that the growth of some fetuses had been retarded by winter severity. A consequence of slower fetal growth due to severe winter weather is the underestimation of fetal age and subsequent overestimation of conception date. The use of an incorrect growth function would also result in a relationship between estimated conception date and fetal age. Variation in the distribution without an accompanying impact on estimated conception date suggests that the sibling variability observed from white-tailed deer fetuses ≤322 mm in length is inherent rather than

environmentally induced. Although estimated conception date was not influenced by age for the fetal sizes examined in this study, the potential influence of these sources of bias should always be considered when estimating conception date.

White-tailed deer fetuses from southwestern Manitoba were found to grow faster than those from Michigan (Short 1970) when singletons and siblings were treated as independent observations. Again, Short (1970) may have underestimated growth rate during the linear phase because her growth function included fetuses from a wide age range. Utilization of each sibling as an observation tends to overstate df and resulted in a liberal estimate of alpha because data from each doe are not weighted equally (eg., a doe with triplets produces 3 observations). Additionally, and unlike subsequent years, a large number of observations of siblings from 1978-79 were indicated to have been the same length (Milliken 1979a) which suggests that differences in length were not documented. If this did occur, growth rate and variance estimates would likely have been impacted minimally. Although litter size was not found to influence growth rate, an effect likely occurs (Hamilton et al. 1985, Verme 1989) such that growth rate would have been influenced through the combination of data irrespective of litter size. Additionally, the growth rate estimated in this study was likely maximized because fetuses >380 mm and those whose doe was deemed to be in poor condition were not included in analyses. In a simulation with a conception distribution based on Ransom (1966), Soprovich (In press) found that growth rate was unbiased for sampling between 64 and 164 days after the mean conception date (i.e., method 2, dates 164-264). The sampling period used in this study was relatively narrow which suggests that the estimate of growth rate was unbiased and that a wider sampling period could have been used without unduly influencing the estimate. Sex and litter effects were relatively minor when Soprovich (In press) mimicked these effects by simulating individual variation; however, they were likely minor due to the high quality food available to the does (Hamilton et al. 1985) and lack of influence of maternal condition on the fetal data used in the simulation.

For a population of deer whose total body fat could be predicted by the Kidney Fat Index or KFI (Finger et al. 1981), Cothran et al. (1987) found the KFI at conception and the rate of fat loss, as indicated by the KFI, to be greater for does with twins than those with singletons and for early-breeding does than late-breeding does. Although their conclusions may have been

influenced by small samples, late-breeding does and those with singletons were not found to exhibit a loss of fat with time (Cothran et al. 1987) which suggests that these groups may have been similar in composition (i.e., that many late breeders also had singletons). Additionally, Cothran et al. (1987) suggested that late-breeding and the conception of a singleton were related to total body fat of the doe at conception which further suggests that the conception date for singletons and twins might differ. In this study, the combination of data irrespective of litter size might bias estimates if mean conception date and litter size were related.

Although variation between siblings is ignored, the more conservative analysis of growth rate with mean forehead-rump length should impact estimates minimally as variation results primarily from day of death. Although fetal growth from Manitoba and Michigan white-tailed deer was not found to differ for this analysis, the observed difference was almost significant at $P = 0.05$ for the data set which combined singletons, twins, and triplets. Given the low precision of the estimate with this method and sample size, the observed alpha is quite low. The progressive increase in alpha with the addition of singletons, and then triplets, may only reflect the increased df as it may not be appropriate to combine litter sizes for growth rate estimation. Additionally, alpha was slightly liberalized by not treating the growth rate of fetuses from Michigan white-tailed deer as an estimate. The differential annual sampling intensity which occurred also had the potential to seriously impact growth rate estimation at the sample size available (eg., a relatively large number of fetuses from late dates might have come from a year when conception was earlier than usual). Additionally, the impact of the environment on the linear growth of fetuses <380 mm long would have acted to depress the estimates of linear growth rate. While these factors suggest that growth rate estimates should be treated cautiously, the evidence also strongly suggests that fetuses from Manitoba adult white-tailed deer may grow faster than those from the Michigan deer examined by Verme (1963) and Short (1970). As conception distribution is constrained environmentally (Soprovich In press), even within Manitoba (i.e., Ransom (1966) provides data which suggests that does from the Duck Mountain area conceive relatively synchronously), it should not be surprising that fetal growth rate might also exhibit considerable geographic variation for this extremely plastic species. To substantiate this conclusion relative to Michigan deer or for any population,

further data should be collected while controlling potentially confounding effects as much as possible. It would also be useful to examine, by simulation, the influence of combining data irrespective of litter size on growth rate estimation, given the assumption that conception date and litter size are related.

Linear growth of all fetuses <440 mm long and twin fetuses <380 mm long was depressed by excessive snow which supports the statement by Milliken (1979a) that "Autopsies showed marked differences in lengths and weights of fetuses of does in poor condition and carrying two or more fawns ...". Snow depth almost certainly acted on fetal growth through its influence on food resources and subsequent doe condition (Hobbs 1989) because birth weight is related to the food resources available to the doe (Verme 1963). Verme (1963) was not able to document a depression in the linear growth of fetuses <380 mm in length, perhaps because his does were in better condition at a comparable time in gestation. The lack of influence of doe visual femur fat on fetal linear growth provides further evidence to support the contention that visual femur fat is both a crude and inaccurate indicator of condition (D. W. Soprovich, unpubl. data). Fetal growth rate was not influenced by temperature; however, the strong correlation between snow depth and temperature makes it difficult to assess the independent effects of these variables. The fetuses from winters with substantial snow accumulation came primarily from 1 winter (eg., 4 observations from 1978/79 for the data set of twins) and were collected primarily from late dates (eg., of the 5 observations of twins with the greatest cumulative snow depth, 4 were from late dates). A consequence of this non-random sampling distribution and the small sample size is that observed results could be due to a relatively large number of observations having come from late-conceived, small fetuses during those years when snow accumulation was great. Again, this potential sampling problem is the consequence of data collection which is fortuitous rather than guided by an experimental design, and verification of snow effects would be strengthened by an experimental approach. The potential of the environment to impact linear fetal growth indicates that estimation of fetal age and conception date, even for fetuses with forehead-rump length <380 mm, can produce biased results similar to those found by Bartmann (1986) for mule deer.

Yearling Does

Contrary to Hamilton et al. (1985) for fetuses from does aged 1.5 to 3.5 years, the linear growth of fetuses from yearling does was not shown to be influenced by sex. Similarly, fetal growth rate was not found to differ from that of fetuses from adult Manitoba does or Michigan does, or to be influenced by snow accumulation or visual femur fat of the doe. The lack of influence of doe condition is somewhat surprising because several does with large fetuses were from a winter with substantial snow accumulation (1978-79) and were in poor condition (i.e., visual femur fat of 1%, 1%, 2.5%, and 40%). This result might be interpreted as support for Verme (1963) who suggested that fetuses ≤150 days old were not influenced by doe condition; however, Verme (1963) used adult does which were likely in better condition at the same stage of gestation. It is far more likely that the inability to detect an impact resulted from the small sample of yearlings and non-random sampling distribution (i.e., the fetuses from 1978-79 may have been impacted by doe condition and/or conceived early), as supported by a poor linear relationship between forehead-rump length and date, an estimated rate of fetal growth (3.123 mm/day) consistent with an environmental impact, and a relationship between fetal weight and length which appears consistent with an environmental impact. Additionally, fetal growth should be impacted earlier in yearlings if this age class is the most sensitive indicator of range conditions, as suggested by Ransom (1967).

The mean conception date of yearlings (21 November) was similar to that of most fawns (26 November) and adults (25 November) when estimated from the linear growth functions. With Short's growth function, the mean conception date of yearlings (27 November), adults (17 November), and most fawns (12 December) was estimated to differ considerably. Again, results for yearlings are extremely tentative due to the small sample size, large differences between siblings of several twins, poor condition of several does, and the many factors previously discussed relative to fetuses from adult does. To accurately estimate fetal growth rate in yearling does from southwestern Manitoba, it is clear that further data are required.

Weight-Length Relationships

Weight increased as a function of length in a manner best described by the power model ($y = B_0 x^{B1}$) for fetuses from adult does. Verme (1989)

reported data suggestive that males and females might differ in birth weight which provides limited support to the hypothesis that the fetal weight-length relationship varies with sex. Sex did not influence the rate of increase for fetuses ≤445 mm or ≤322 mm in length; however, the comparison of fetuses ≤445 mm long was weak because 7 of the 9 fetuses >322 mm long were males. Although a sex-related effect was not detected in this study, P values suggest the need for an increased sample size to properly evaluate this possibility. As linear fetal growth (Hamilton et al. 1985) and birth weight (Verme 1989) are influenced by litter size, and as it appears that the weight of fetuses >133 days old can be affected by doe condition (Verme 1963), the inclusion of singletons, twins, and triplets to 445 mm in length likely resulted in a low estimate for the rate of increase.

There were not enough data to properly assess the relationship between the weight and length of fetuses from yearling does. In particular, fetuses from yearlings were relatively light and the weights and lengths examined were from a range for which the relationship was approximately linear in adult does. Additionally, the small sample size almost precluded the possibility of detecting a difference in the relationship between fetuses from yearling and adult does. The hypothesis that doe age might influence this relationship is supported somewhat by the fact that birth weight varies with maternal age (Verme 1989). Although there were not enough data to adequately examine the influence of maternal condition on the fetal weight-length relationship, it is noteworthy that of the 6 largest fetuses, those from a doe with 10% visual femur fat were light ($n = 2$, $\bar{x} = 440$ mm, $\bar{x} = 2025$ g) as compared to the others ($n = 4$, $\bar{x} = 436$ mm, $\bar{x} = 2396$ g). This suggests that condition of these does may have influenced the weight-length function for fetuses ≤445 mm long.

RECOMMENDATIONS

1. Studies to determine variation in gross productivity will provide data of little value to white-tailed deer population management and should not be conducted. Rather than attempting to document small differences in gross productivity, variation in net productivity should be monitored to provide useful management data and to determine the relationship between recruitment and winter weather severity. Net productivity could be monitored via the hunter questionnaire, line

transect, or deer observer methods; however, it must be recognized that each of these forms of estimation would be subject to bias (eg., see Soprovich 1990), perhaps substantial in magnitude, and that such bias can limit the application of resultant estimates (eg., they often will not be appropriate for simple population models).

2. Seasonality of breeding should be examined on the basis of ovarian follicular changes.
3. Fetal growth rate under optimum conditions and the relationship between doe condition, fetal growth rate, and recruitment should be determined. Such information would not only provide a useful population management tool but would allow for a rational method for determining which fetuses could not be used to estimate conception date because of doe nutritional effects.

LITERATURE CITED

Armstrong, R.A. 1950. Fetal development of the northern white-tailed deer (Odocoileus virginianus borealis Miller). Am. Nat. 43:650-666.

Bartmann, R.M. 1986. Growth rates of mule deer fetuses under different winter conditions. Great Basin Nat. 46:245-248.

Cheatum, E.L. 1949. Bone marrow as an index of malnutrition in deer. N. Y. State Conserv. 3:19-22.

Cheatum, E.L., and G.H. Morton. 1946. Breeding season of white-tailed deer in New York. J. Wildl. Manage. 10:249-263.

Chranowski, D.J. 1982a. 1982 white-tailed deer carcass study in the Southwestern Region. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 82-21. 14 pp.

Chranowski, D.J. 1982b. Winter weather and white-tailed deer in the Southwestern Region - 1982. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 82-24. 33 pp.

Chranowski, D.J. 1983a. 1983 white-tailed deer carcass study in the Southwestern Region. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 83-19. 24 pp.

Chranowski, D.J. 1983b. Winter weather and white-tailed deer in the Southwestern Region - 1983. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 83-18. 34 pp.

Chranowski, D.J. 1984a. 1984 white-tailed deer carcass study in the Southwestern Region. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 84-14. 15 pp.

Chranowski, D.J. 1984b. Winter weather and white-tailed deer in the Southwestern Region - 1984. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 84-13. 36 pp.

Chranowski, D.J. 1985a. 1985 white-tailed deer carcass study in the Southwestern Region. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 85-12. 23 pp.

Chranowski, D.J. 1985b. Winter weather and white-tailed deer in the Southwestern Region - 1985. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 85-14. 47 pp.

Clutton-Brock, T.J. 1985. Reproductive success in red deer. Sci. Am. 252:86-92.

Cothran, E.G., R.K. Chesser, M.H. Smith, and P.E. Johns. 1987. Fat levels in female white-tailed deer during the breeding season and pregnancy. J. Mammal. 68:111-118.

Finger, S.E., I.L. Brisbin Jr., and M.H. Smith. 1981. Kidney fat as a predictor of body condition in white-tailed deer. J. Wildl. Manage. 45:964-968.

Frish, R.E. 1988. Fatness and fertility. Sci. Am. 258(3):88-95.

Glass, G.V., P.D. Peckham, and J.R. Sanders. 1972. Consequences of failure to meet assumptions underlying the fixed effects analysis of variance and covariance. Rev. Educ. Res. 42:237-288.

Hall, M.H., and E.C. Hall. 1980. An early-born fawn in New York. N. Y. Fish Game J. 27:103.

Hamilton, R.J., M.L. Tobin, and W.G. Moore. 1985. Aging fetal white-tailed deer. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies. 39:389-395.

Hobbs, N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildl. Monogr. No. 101. 39 pp.

Johns, P.E., M.H. Smith, and R.K. Chesser. 1984. Annual cycles of the kidney fat index in a southeastern white-tailed deer herd. J. Wildl. Manage. 48:969-973.

Kerr, K.D., and W.J. Peterson. 1988. Late breeding in the white-tailed deer, Odocoileus virginianus, in Northern Minnesota. Can. Field-Nat. 102:552-553.

Kleinbaum, D.G., and L.L. Kupper. 1978. Applied regression analysis and other multivariable methods. Wadsworth Publishing Company, Inc., Belmont, California. 556 pp.

Larson, J.S., and R.D. Taber. 1980. Criteria of sex and age. Pages 143-202 in S.D. Schemnitz, ed. Wildlife management techniques manual. Fourth ed. The Wildl. Soc., Washington, D.C. 686 pp.

Mendenhall, W. 1971. Introduction to probability and statistics. Third ed. Wadsworth Publishing Company, Inc., Belmont, California. 466 pp.

Milliken, I.J. 1977a. 1977 white-tailed deer carcass study in the Brandon Sub-Region. Manitoba Dept. Renew. Resour. Trans. Serv. Tech. Rep. No. 77-4. 8 pp.

Milliken, I.J. 1977b. Winter weather and white-tailed deer in the Brandon Sub-Region - 1973 to 1976. Manitoba Dept. Renew. Resour. Trans. Serv. Tech. Rep. No. 77-2. 26 pp.

Milliken, I.J. 1978a. 1978 white-tailed deer carcass study in the Brandon Sub-Region. Manitoba Dept. Renew. Resour. Trans. Serv. Manuscr. Rep. No. 78-58. 19 pp.

Milliken, I.J. 1978b. Winter weather and white-tailed deer in the Brandon Sub-Region - 1978. Manitoba Dept. Renew. Resour. Trans. Serv. Manuscr. Rep. No. 78-59. 33 pp.

Milliken, I.J. 1979a. 1979 white-tailed deer carcass study in the Brandon Sub-Region. Manitoba Dept. Mines Nat. Resour. Environ. Manuscr. Rep. No. 79-70. 22 pp.

Milliken, I.J. 1979b. Winter mortality and white-tailed deer in the Brandon Sub-Region - 1979. Manitoba Dept. Mines Nat. Resour. Environ. Manuscr. Rep. No. 79-67. 34 pp.

Milliken, I.J. 1980a. 1980 white-tailed deer carcass study in the Southwestern Region. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 80-21. 16 pp.

Milliken, I.J. 1981a. 1981 white-tailed deer carcass study in the Southwestern Region. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 81-17. 15 pp.

Milliken, I.J. 1981b. Winter weather and white-tailed deer in the Southwestern Region - 1980 and 1981. Manitoba Dept. Nat. Resour. Manuscr. Rep. No. 81-18. 45 pp.

Nelson, M.E., and L.D. Mech. 1986. Mortality of white-tailed deer in northeastern Minnesota. J. Wildl. Manage. 50:691-698.

Oftedal, O.T. 1985. Pregnancy and lactation. Pages 215-238 in R.J. Hudson and R.G. White, eds. Bioenergetics of wild herbivores. CRC Press, Inc., Boca Raton, Florida. 314 pp.

Ozoga, J.J., and L.J. Verme. 1985. Determining fetus age in live white-tailed does by x-ray. J. Wildl. Manage. 49:372-374.

Parker, K.L., C.T. Robbins, and T.A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474-488.

Ransom, A.B. 1964. Reproductive biology of white-tailed deer in Manitoba. M.Sc. Thesis, Univ. Alberta, Edmonton. 75 pp.

Ransom, A.B. 1966. Breeding seasons of white-tailed deer in Manitoba. Can. J. Zool. 44:59-62.

Ransom, A.B. 1967. Reproductive biology of white-tailed deer in Manitoba. J. Wildl. Manage. 31:114-123.

Sauer, P.R., and C.W. Severinghaus. 1983. Relationship of degree and composition of winter mortality of deer, as indicated by strip surveys, to severity of the winter. N. Y. Fish Game J. 30:173-181.

Short, C. 1970. Morphological development and aging of mule deer and white-tailed deer fetuses. J. Wildl. Manage. 34:383-388.

Soprovich, D.W. In press. Fetal growth rate estimation from length and date of death. In R.D. Brown, ed. The biology of deer. Springer-Verlag, Inc., New York, New York.

Soprovich, D.W. 1990. The Verme weather severity index, harvest statistics, and white-tailed deer (Odocoileus virginianus) in southwestern Manitoba. Man. Dept. Nat. Resour. Tech. Rep. No. 90-03. 32 pp.

Strickberger, M.W. 1968. Genetics. Third ed. The Macmillan Company, New York, New York. 868 pp.

Taber, R.D. 1963. Criteria of sex and age. Pages 119-189 in H.S. Mosby, ed. Wildlife investigational techniques. Second ed. The Wildl. Soc., Washington, D.C. 419 pp.

Torbit, S.C., L.H. Carpenter, D.M. Swift, and A.W. Alldredge. 1985. Differential loss of fat and protein by mule deer during winter. J. Wildl. Manage. 49:80-85.

Torbit, S.C., L.H. Carpenter, R.M. Bartmann, A.W. Alldredge, and G.C. White. 1988. Calibration of carcass fat indices in wintering mule deer. J. Wildl. Manage. 52:582-588.

Verme, L.J. 1962. Mortality of white-tailed deer fawns in relation to nutrition. Proc. Deer Disease Symp. 1:15-32.

Verme, L.J. 1963. Effect of nutrition on growth of white-tailed deer fawns. Trans. N. Am. Wildl. Conf. 28:431-443.

Verme, L.J. 1968. An index of winter weather severity for northern deer. J. Wildl. Manage. 32:566-574.

Verme, L.J. 1977. Assessment of natal mortality in Upper Michigan deer. J. Wildl. Manage. 41:700-708.

Verme, L.J. 1985. Birth weights of fawns from doe fawn white-tailed deer. J. Wildl. Manage. 49:962-963.

Verme, L.J. 1989. Maternal investment in white-tailed deer. J. Mammal. 70:438-442.